EVOLUTION

INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

PUBLISHED BY

THE SOCIETY FOR THE STUDY OF EVOLUTION

Vol. VIII DECEMBER, 1954 No. 4

EXPERIMENTAL STUDIES OF THE DISTRIBUTION OF GENE FREQUENCIES IN VERY SMALL POPULATIONS OF DROSOPHILA MELANOGASTER. III. ARISTAPEDIA AND SPINELESS

WARWICK E. KERR AND SEWALL WRIGHT

Universidade de São Paulo and the University of Chicago

Received February 23, 1954

HISTORY BY GENERATION

This experiment involves the histories of 113 lines, all started from groups of 4 s/a females and 4 s/a males (using s and a for the alleles spineless (ss) and aristapedia (ss^a) for simplicity). These were continued by random selection of 4 females and 4 males for 10 generations, except for 7 lines in which spineless became fixed. An additional line became fixed in this respect in the 10th generation. The distributions of number of aristapedia genes in each set of 8 flies is shown by generation in table 1, together with averages and variances of gene frequencies for each generation, excluding those previously fixed. The small number fixed is in marked contrast with the results with forked and Bar discussed in previous papers and is undoubtedly due to strong selection against both homozygous types, relative to the heterozygotes.

The mean gene frequency of aristapedia fell from initial .50 to .3544 in generation 5 among those in which fixation had not occurred but then rose somewhat to an average in the last 3 generations (.4032) which was substantially the same as that in generation 2 (.4043). The variance reached .0235 in 2 generations and fluctuated about this thereafter. A χ^2 test for homogeneity from generation 2 to 10 (excluding previously fixed lines, and grouping frequencies 0 and 1, and 11 to 14) gives $\chi^2 = 61.5$, n = 80, probability .94. Practically, we may consider that the distribution reached equilibrium of form in 2 generations with a mean gene frequency of $.3882 \pm .0049$ and a standard deviation of $.1536 \pm .0035$.

SELECTION COEFFICIENTS

If there were no differences in viability, generation 1 should consist of 25% a/a, 50% a/s and 25% s/s. The actual percentages (17.92:56.75:25.33) differ

Experimental data by W. E. Kerr under a fellowship of the Rockefeller Foundation, mathematical analysis by S. Wright. Acknowledgment is made to Dr. Th. Dobzhansky for material and for his hospitality during the conduct of these experiments. Acknowledgment is also made to Dr. J. F. Crow for material and suggestions. Analysis was aided by a grant from the Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago.

TABLE 1. *The distribution of numbers of aristapedia genes, represented in each generation among 113 lines, consisting of 4 females, 4 males each.* Newly fixed spineless is distinguished from previously fixed spineless.

	Generation											Total 2–10
	0	1	2	3	4	5	6	7	8	9	10	
Old 0					(1)	(4)	(4)	(4)	(5)	(6)	(7)	
New 0				1	3			1	1	1	1	8
1			2	3	1	2	2	3	1	3	1	18
2		1	5	5	4	8	4	0	3	3	5	37
3		1	6	9	9	10	6	8	6	8	10	72
4		10	10	8	17	12	13	11	15	12	7	105
5		11	15	17	13	19	19	17	15	10	13	138
6		11	17	18	18	18	19	24	14	14	19	161
7		22	22	21	18	16	16	14	17	18	12	154
8	113	22	17	12	16	14	12	12	14	14	16	127
9		20	8	10	6	7	12	9	7	10	10	79
10		7	3	5	2	1	4	7	9	10	6	47
11		6	6	3	3	2	1	2	2	2	3	24
12		1	1	1	0		1	1	2	1	1	8
13		1	0		1				2	1	2	6
14			1		1							2
Total	113	113	113	113	112	109	109	109	108	107	106	986
$\bar{q}$	.5000	.4629	.4043	.3833	.3711	.3544	.3830	.3893	.4051	.4030	.4015	.3882
σ_q^2	0	.01707	.02351	.02333	.02515	.01896	.01932	.02095	.02603	.02677	.02693	.02350

significantly (probability <.001) and indicate viabilities of 63% for a/a and 89% for s/s relative to that for a/s. There is probably also a slight difference between males and females (probability about .04) in the viabilities of the homozygotes relative to the heterozygotes of the same sex. The present data give no indication of the true relative viabilities of males and females.

	a/a	a/s	s/s
Males	.525	1	.965
Females	.740	1	.819
Average	.632	1	.893

As these data are from a compact group which may not reflect accurately the situation in later generations, the ratios were obtained from all sets of 8 flies from generations 2 to 10, the parents of which consisted of 4 a/s females and 4 a/s males (table 2). These differed even more from expected 1:2:1 than did generation 1 (viability 47% for a/a and 57% for s/s relative to a:s). The difference from generation 1 is probably significant (probability .04). Table 2 also shows the ratios from other vials in which gene frequency was .50 in both sets of parents but in which one or both sets consisted of 1 a/a:2 a/s:1 s/s instead of 4 a/s in both sexes. In these cases, deviations from the 1:2:1 ratio among offspring may involve differential productivity of a/a and s/s relative to a/s as well as differential viability among the offspring. There is, however, no significant difference between (121–040) and (040–040) (females first in order a/a, a/s, s/s, males following in the same order) probability .80–.90, or between 121–121 and 040–121 (probability .10–.20) but these two groups differ significantly from each other (probability <.01). It appears that there can not be much difference between a/a and s/s females in productivity but that a/a males are much less productive than s/s males under the conditions of these experiments. When the fathers consisted of 1 a/a:2 a/s:1 s/s,

the ratio among the offspring (19 a/a: 146 a/s:67 s/s) includes fewer a/a and more s/s than expected if a/a males were completely nonproductive and s/s males were as productive as a/s males (22.2 a/a:151.8 a/s:58.0 s/s if .50a:50s eggs). These data are not, however, numerous enough for reliable determinations of relative productivities.

The remaining data include so many types of mating with such entanglement of possible differences in productivity of a/a and s/s relative to a/s in both sexes that an analysis of the sort used in the much simpler sex-linked case of Bar did not seem practicable. We have, however, taken out 4 fairly large, moderately homogeneous groups to obtain rough estimates. In group E (table 3) 2 or 3 a/a female parents competed with at least one a/s female, but only one if any a/a male was present in the set of 4 males. Group F gives the same sort of test for an excess of a/a males. In group G, there were 2 or 3 s/s females competing with at least one a/s female while only one if any s/s male and only one if any a/a male were present. The last condition prevents overlap with group F. Group H is similar with reversal of the sexes and thus designed to test productivity with an excess of s/s males present.

The average gene frequency of aristapedia is naturally rather high among the parents in E and F (.590, .585 respectively) and much lower in G and H (.346, .345 respectively). The offspring regress strongly toward the population average in all cases (.470 in E, .432 in F, .360 in G, and .400 in H). Using unweighted averages, it appears that the parental difference between the two groups (.242) is reduced to only 29% of its value (.071) in the offspring, indicating an average selection of more than 70% against the homozygotes. The greatest deviation from the parental average is in F, again indicating complete or nearly complete failure of a/a males to produce in competition with a/s males, but the results in E indicate low productivity of a/a females also. The most nearly normal productivity of homozygotes seems to be that of s/s females, in excess in G.

With these indications as a starting point, sets of productivity coefficients were applied to the parental frequencies in E to H and constant viability coefficients were applied to the frequencies of the zygotes from random union of the

TABLE 2. *Offspring from vials in which the parents were of the types indicated at the tops of the columns*

	F_1 ♀ 040 ♂ 040		F_2-F_{10} Total		A ♀ 040 ♂ 040		B ♀ 121 ♂ 040		C ♀ 040 ♂ 121		D ♀ 121 ♂ 121		A-D	
	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%
♀ a/a	94	20.8	434	11.0	19	18.3	12	13.6	6	9.4	4	7.7	41	13.3
a/s	254	56.2	2281	57.8	66	63.4	59	67.1	46	71.9	32	61.5	203	65.9
s/s	104	23.0	1229	31.2	19	18.3	17	19.3	12	18.7	16	30.8	64	20.8
♂ a/a	68	15.0	389	9.9	13	12.5	12	13.6	4	6.3	5	9.6	34	11.0
a/s	259	57.3	2198	55.7	71	68.3	59	67.1	42	65.6	26	50.0	198	64.3
s/s	125	27.7	1357	34.4	20	19.2	17	19.3	18	28.1	21	40.4	76	24.7
No.	904		7888		208		176		128		104		616	
q_a ♀		48.9		39.9		50.0		47.2		45.3		38.5		46.3
♂		43.7		37.7		46.6		47.2		39.1		34.6		43.2
Tot.		46.3		38.8		48.3		47.2		42.2		36.5		44.7

arrays of eggs and sperms estimated in each case. It appears that the viability coefficients (not distinguishing those of males and females) must be close to .50 for a/a and .75 for s/s to account for the percentages of heterozygotes. These are lower than indicated in F_1, but not so low as indicated by the progeny of a/s females with a/s males of later generations. The productivity coefficients are easily narrowed by trial to the nearest .05. These indicate relative productivities of a/a, a/s and s/s females of about .40:1:.75 respectively of a/a, a/s and s/s males of 0:1:.25 respectively under the conditions in these groups of parents.

The agreement with observed numbers of offspring (table 4) is not good ($\chi^2 = 13.3$) but from inspection of the differences, it is evident that no single set of productivity and viability coefficients can account well for the results in H and the others. H seems to require lower viability coefficients. Similarly application of the above set of coefficients to groups A to D also gives a poor fit ($\chi^2 = 13.9$) but this is considerably improved by using .40:1:.60 for the viability coefficients of a/a, a/s and s/s respectively. If the single set of 6 coefficients based on E to H is applied to all 8 groups, $\chi^2 = 27.2$, n = 10, probability .001 to .01. This could no doubt be improved a little by deriving the coefficients with maximum probability from all of these data but it is obvious that there must be complications either in assortative mating or heterogeneity.

Possible sex differences in viability, indicated in the data from the first generation, have been ignored above. Groups A to D collectively do not show significant differences in the frequencies of the sexes and the same is true of E to H collectively. In both cases, however, there is a suggestion that aristapedia has somewhat lower viability and spineless somewhat higher viability in males than in females, relative to a/s in both, in agreement with the data from the first generation. Even on combining A to H the distributions of the sexes differ only enough to give $\chi^2 = 4.42$, probability .10 to .20. It is necessary to consider the

TABLE 3. *Offspring from vials in which the parents were in the categories indicated at the tops of the columns.* The exact composition of the parental as well as the offspring populations are shown in the columns.

	E				F				G				H			
	♀: 2,3 a/a, 1,2 a/s ♂: 0,1 a/a				♀: 0,1 a/a ♂: 2,3 a/a, 1,2 a/s				♀: 2,3 s/s, 1,2 a/s ♂: 0,1 s/s, 0,1 a/a				♀: 0,1 s/s, 0,1 a/a ♂: 2,3 s/s, 1,2 a/s			
	Parents		Offspring		Parents		Offspring		Parents		Offspring		Parents		Offspring	
	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%	no.	%
♀ a/a	171	54.1	57	18.0	21	11.9	29	16.5	24	4.5	38	7.2	45	7.2	57	9.1
a/s	118	37.3	190	60.1	117	66.5	105	59.7	210	39.8	304	57.6	474	76.0	396	63.5
s/s	27	8.6	69	21.8	38	21.6	42	23.9	294	55.7	186	35.2	105	16.8	171	27.4
♂ a/a	46	14.6	48	15.2	92	52.3	24	13.6	39	7.4	40	7.6	26	4.2	56	9.0
a/s	194	61.4	194	61.4	69	39.2	93	52.8	395	74.8	300	56.8	245	39.3	376	60.3
s/s	76	24.0	74	23.4	15	8.5	59	33.5	94	17.8	188	35.6	353	56.6	192	30.8
No.	632		632		352		352		1056		1056		1248		1248	
q_a ♀		72.8		48.1		45.2		46.3		24.4		36.0		45.2		40.9
♂		45.3		45.9		71.9		40.1		44.8		36.0		23.8		39.1
Tot.		59.0		47.0		58.5		43.2		34.6		36.0		34.5		40.0

TABLE 4. *The observed numbers of offspring of genotypes a/a, a/s and s/s in groups A to H and the expected number, assuming productivity in females of genotypes a/a, a/s and s/s in the ratio .40:1:.75 respectively, productivity of males of 0:1:.25 in the same order, and viability coefficients in both sexes of .50 for a/a:1 for a/s: .75 for s/s*

		o	c	o-c	$\frac{(o-c)^2}{c}$			o	c	o-c	$\frac{(o-c)^2}{c}$
E	a/a	105	109.9	− 4.9	.22	A	a/a	32	32.0	0	0
	a/s	384	399.5	−15.5	.60		a/s	137	128.0	+ 9.0	.63
	s/s	143	122.6	+20.4	3.39		s/s	39	48.0	− 9.0	1.69
F	a/a	53	44.1	+ 8.9	1.80	B	a/a	24	23.9	+ 0.1	0
	a/s	198	212.5	−14.5	.99		a/s	118	107.4	+10.6	1.05
	s/s	101	95.4	+ 5.6	.32		s/s	34	44.7	−10.7	2.56
G	a/a	78	77.2	+ 0.8	.01	C	a/a	10	17.4	− 7.4	3.15
	a/s	604	610.9	− 6.9	.08		a/s	88	78.1	+ 9.9	1.25
	s/s	374	367.9	+ 6.1	.10		s/s	30	32.5	− 2.5	.19
H	a/a	113	123.4	−10.4	.88	D	a/a	9	12.5	− 3.5	.98
	a/s	772	730.2	+41.8	2.39		a/s	58	62.3	− 4.3	.30
	s/s	363	394.4	−31.4	2.50		s/s	37	29.2	+ 7.8	2.08
Total		3288	3288.0	0	13.28	Total		616	616.0	0	13.88
Total	a/a	349	354.6	− 5.6	.09	Total	a/a	75	85.8	−10.8	1.36
	a/s	1958	1953.2	+ 4.8	.01		a/s	401	375.8	+25.2	1.69
	s/s	981	980.3	+ 0.7	0		s/s	140	154.4	−14.4	1.34

total distribution from generations 2 to 10 to obtain a significant difference (probability .01 to .02). These data are too heterogeneous for more than rough estimates. Assume that the zygotic frequencies $f_{aa(Z)}$, $f_{as(Z)}$ and $f_{ss(Z)}$ are the same in the sexes. Let $f_{aa(F)}$ and $f_{aa(M)}$ be the observed frequencies of a/a females and males respectively and similarly for a/s and s/s.

$$\frac{f_{aa(F)}}{f_{as(F)}} = \frac{f_{aa(Z)}V_{aa(F)}}{f_{as(Z)}}, \quad \frac{f_{aa(M)}}{f_{as(M)}} = \frac{f_{aa(Z)}V_{aa(M)}}{f_{as(Z)}}$$

The ratio $R_{aa} = V_{aa(M)}/V_{aa(F)}$ can now be obtained.

$$R_{aa} = \frac{V_{aa(M)}}{V_{aa(F)}} = \frac{f_{aa(M)}f_{as(F)}}{f_{as(M)}f_{aa(F)}}$$

$$R_{ss} = \frac{V_{ss(M)}}{V_{ss(F)}} = \frac{f_{ss(M)}f_{as(F)}}{f_{as(M)}f_{ss(F)}}$$

For F_2 to F_{10}, $R_{aa} = .930$, $R_{ss} = 1.146$. Letting

$$\bar{V}_{aa} = \tfrac{1}{2}(V_{aa(F)} + V_{aa(M)})$$
$$V_{aa(F)} = 2\bar{V}_{aa}/(1 + R_{aa})$$
$$V_{aa(M)} = 2\bar{V}_{aa} - V_{aa(F)}$$

Adopting

$$\bar{V}_{aa} = .50$$
$$V_{aa(F)} = .52, \quad V_{aa(M)} = .48$$

Similarly if

$$\bar{V}_{ss} = .75$$
$$V_{ss(F)} = .70, \quad V_{ss(M)} = .80$$

THE DISTRIBUTION OF GENE FREQUENCIES

In cases in which viability differences are small, in which the productivity coefficients of the various genotypes are sufficiently similar in males and females to be averaged without important errors, and in which mating is random, the average rate of change of gene frequency (Δq) can be expressed as a simple function of the gene frequency and the selection coefficients (Wright and Dobzhansky, 1946).

	f(frequency)	*W* (selection value)	
a/a	q^2	$1 - s$	$\bar{W} = 1 - sq^2 - t(1 - q)^2$
a/s	$2q(1 - q)$	1	$\Delta q = \frac{q(1 - q)}{2\bar{W}} \frac{d\bar{W}}{dq} = -(s + t)q(1 - q)(q - \hat{q})/\bar{W}$
s/s	$(1 - q)^2$	$1 - t$	$\hat{q} = t/(s + t)$

The distribution of gene frequencies at equilibrium is (Wright, 1937):

$$\varphi(q) = (C/\sigma_{\delta q}^2) \exp [2\int (\Delta q/\sigma_{\delta q}^2)dq]$$

If random drift is due solely to accidents of sampling

$$\sigma_{\delta q}^2 = q(1 - q)/(2N)$$

$$\varphi(q) = C\bar{W}^{2N}/q(1-q)$$
$$= C[1-sq^2-t(1-q)^2]^{2N}/q(1-q)$$

In the present data, the situation is obviously much more complicated. The genetic arrays of the sexes differ systematically because of the differences in productivity and to a minor extent viability coefficients. Thus systematic departures from the binomial square law are to be expected among zygotic frequencies even if mating is assumed to be at random. These departures could be ignored in obtaining rough approximations by use of the averages of the coefficients for the sexes (cf. Wright and Dobzhansky, 1946) if it were possible to deal collectively with all populations of the same zygotic gene frequencies. The most serious difficulty arises from the fact that the frequencies of genotypes are determinable only after large but undoubtedly varying proportions of the homozygotes have died. Letting $W_{aa} = V_{aa}U_{aa}$, $W_{ss} = V_{ss}U_{ss}$, $s = 1 - W_{aa}$, $t = 1 - W_{ss}$, where the U's are productivity coefficients.

Zygote	*Imago*	*Gamete*
a/a: q^2	$V_{aa}q^2/D$	*a*: $(q-sq^2)/\bar{W}$
a/s: $2q(1-q)$	$2q(1-q)/D$	*s*: $[1-q-t(1-q)^2]/\bar{W}$
s/s: $(1-q)^2$	$V_{ss}(1-q)^2/D$	
	$D=1-(1-V_{aa})q^2-(1-V_{ss})(1-q)^2$	$\bar{W}=1-sq^2-t(1-q)^2$

The change of gene frequency from zygote to zygote and the distribution of zygotic gene frequencies are (approximately) as given above but the change of gene frequency from imago to imago and the distribution of the gene frequencies in imagoes can not be expressed in simple form. The zygotic q is here a quadratic function of the imaginal q.

We may, however, as in the case of Bar (Part II of this series), find an empirical relation between imaginal gene frequency and the change in the following generation. Table 5 shows the mean change in gene frequency in the offspring for each class of parental gene frequencies (generations 1 to 9), the variance of these changes ($\sigma_{\delta q}^2$) and the ratio $q(1 - q)/\sigma_{\delta q}^2$ which would indicate effective $2N_e$ if zygotic gene frequencies were in question and variability were due only to accidents of sampling.

Change of gene frequency is plotted against parental gene frequency in figure 1. From the form it appears that the formula, applicable to zygotic frequencies may give an adequate empirical fit. A rough evaluation of the coefficients can be obtained as described previously (Wright and Dobzhansky, 1946) from the regression of Δq on q in the nearly straight middle portion of the

curve.

$$\frac{1}{\bar{W}} = 2\left(1+\frac{\Delta q}{\bar{q}}\right)\left(1-\frac{\Delta q}{1-\bar{q}}\right) - 1 - b_{\Delta q \cdot q}$$

$$s = \frac{1}{\bar{q}}\left[1-\left(1+\frac{\Delta q}{\bar{q}}\right)\bar{W}\right]$$

$$t = \frac{1}{1-\bar{q}}\left[1-\left(1-\frac{\Delta q}{1-\bar{q}}\right)\bar{W}\right]$$

In the present case, the entries from q = 5/16 to q = 12/16 yield $\bar{q}$ = .452, Δq = − .0331, $b_{\Delta q \cdot q}$ = − .568, $\bar{W}$ = .652, s = .875, t = .563, $\hat{q}$ = .392. If parental generation 1 is omitted, s comes out .878 and t .582.

The ratio $q(1-q)/\sigma_{\delta q}^2$ varies irregularly but there is no clear trend except perhaps for small values between q = 1/16 to 4/16. The indicated estimate for $2N_e$ is 13.0 (instead of 16). Even this, however, is undoubtedly too high, since it is based on the variability after the frequencies of homozygotes have been cut down severely by selective viability (a complication that was absent or unimportant in the case of Bar).

If Δq and $\sigma_{\delta q}^2$ for imaginal gene frequencies may be taken as approximating empirically the same functions as for the zygotic frequencies, the distribution of imaginal gene frequencies should be approximated by the formula cited except

TABLE 5. *The observed changes per generation* (Δq) *in relation to gene frequency of parental populations of generations 1 to 9, the calculated values from the formula*

$$\Delta q = -(s+t)q(1-q)(q-\hat{q})/[1-sq^2 - t(1-q)^2],\ s=.86,\ t=.60,\ \hat{q}=t/(s+t),$$

the variance of changes, $\sigma_{\delta q}^2$, *and the ratio* $q(1-q)/\sigma_{\delta q}^2$

16_q	f	q	Δq obs.	Δq calc.	$\sigma_{\delta q}^2$	$\frac{q(1-q)}{\sigma_{\delta q}^2}$
1	17	.0625	+.0882	+.0635	.0127	4.6
2	33	.1250	+.0511	+.0866	.0106	10.3
3	63	.1875	+.0972	+.0867	.0165	9.2
4	108	.2500	+.0689	+.0724	.0192	9.8
5	136	.3125	+.0533	+.0489	.0131	16.5
6	153	.3750	+.0049	+.0191	.0174	13.5
7	164	.4375	−.0312	−.0147	.0165	14.9
8	133	.5000	−.0536	−.0512	.0162	15.4
9	89	.5625	−.1088	−.0888	.0237	10.4
10	48	.6250	−.0950	−.1263	.0233	10.1
11	27	.6875	−.1574	−.1621	.0151	14.2
12	8	.7500	−.2969	−.1938	.0131	14.3
13	5	.8125	−.1750	−.2172	.0147	10.4
14	2	.8750	−.2500	−.2231	.0078	14.0
15	0	.9375	—	−.1863	—	—
	986					13.03

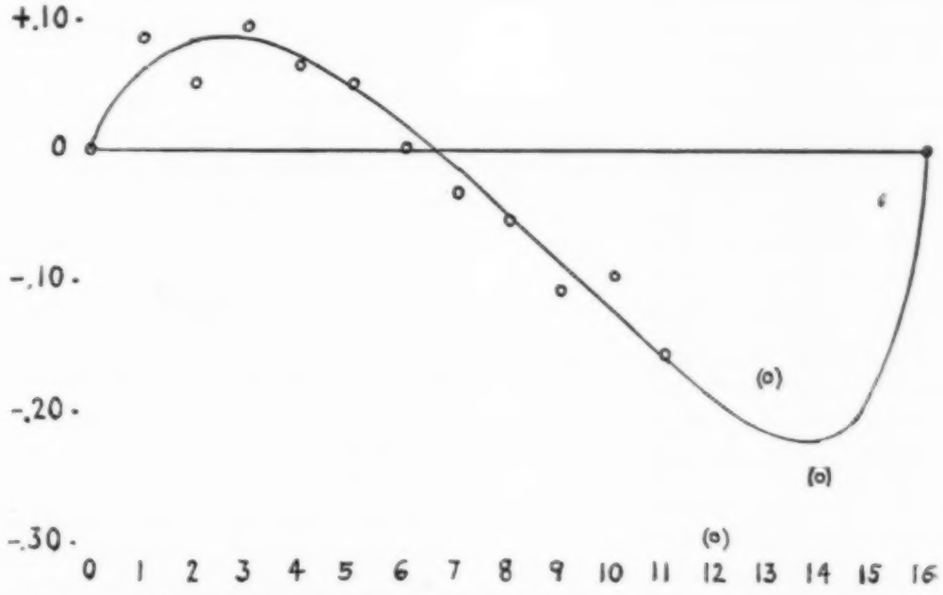


FIG. 1. Observed mean changes of gene frequency in relation to numbers of aristapedia genes in populations of eight flies (small circles) in comparison with those expected from the formula

$$\Delta q = -(s+t)q(1-q)(q-\hat{q})/[1-sq^2-t(1-q)^2];$$
$$s = .86,\ t = .60,\ \hat{q} = .411.$$

for the usual inaccuracy near the extremes in applying a formula based on large 2N to populations with small 2N. The low rate of fixation is ignored.

It turns out that the values s = .88, t = .58 give too small a mean and 2Ne = 13 gives, as expected, too small a variance. It was found by trial that the values s = .86, t = .60, $2N_e = 10.7$ give the best fit without going to a larger number of decimal places. Figure 1 shows how well the values of Δq calculated from these estimates of s and t fit the observed values of Δq. Table 6 and figure 2 show the agreement between the observed and calculated frequencies of the gene frequencies. $\chi^2 = 5.38$, n = 9 (on grouping the small classes 12 to 14), probability .80.

We take this opportunity to correct a typographical error and a confusion between two modes of presentation of certain equations in part II of this series (Evolution VIII, p. 235, right side)

In line 8:

− 4Ns instead of − 4N at beginning

In line 9:

$$q(1 - q)\varphi(q) = e^{2Ns}\chi(q)$$

In line 13:

$$\chi(q) = Cq(1 - q)[1 + C_1q(1 - q)$$

TABLE 6. *The observed frequencies of aristapedia genes in sets of 8 flies (generations 2 to 10) from unfixed parental populations, in comparison with frequencies calculated from s = .86, t = .60, $2N_e = 10.7$*

$16q$	frequency o	frequency c	(o − c)	$\frac{(o-c)^2}{c}$
0	8	10.4	−2.4	.55
1	18	20.9	−2.9	.40
2	37	38.8	−1.8	.08
3	72	68.9	+3.1	.14
4	105	105.7	−0.7	0
5	138	138.8	−0.8	0
6	161	156.3	+4.7	.14
7	154	151.0	+3.0	.06
8	127	124.6	+2.4	.05
9	79	86.9	−7.9	.72
10	47	50.1	−3.1	.19
11	24	23.2	+0.8	.03
12	8	8.1		
13	6	2.0		
14	2	0.3	+5.6	3.02
15	0	0		
16	0	0		
	986	986.0		5.38

DISCUSSION

In natural panmictic populations of ordinary size, genes subject to such enormous selection, as that against Bar in the second paper of this series, would be eliminated too rapidly for random drift from inbreeding to be of appreciable importance. The same is probably true of forked (in the first paper) even though the selection against it was hardly detectible in the small experimental populations. In the case of aristapedia and spineless, the enormous selection against both homozygotes would keep a large population very close to the equilibrium point (about 40% ss^a). We may, however, consider the experimental populations as models, on exaggerated scales with respect to the effects of inbreeding and, in two cases, of selection, of situations that might occur in isolated local populations in nature with respect to a pair of isoalleles or of alleles with primary effects on multifactorial quantitative variability.

In arrays of such populations with effective size one thousand times as great as in the experimental populations, the random drift and ultimate fixation due to inbreeding would occur at only one-thousandth of the rates observed here. The forms of the distributions after approximate stability has been reached (in one thousand times the observed periods) would, however, be nearly the same as observed if selective disadvantage in all cases is only one-tenth of a percent of those in the experiments. Such coefficients are reasonable enough for isoalleles or alleles with primary effects on quantitative variability (Wright, 1952).

The experiments with forked may be considered as giving a model of the inbreeding effect in almost pure form. Those with Bar give a model of the case in which an allele tends toward fixation

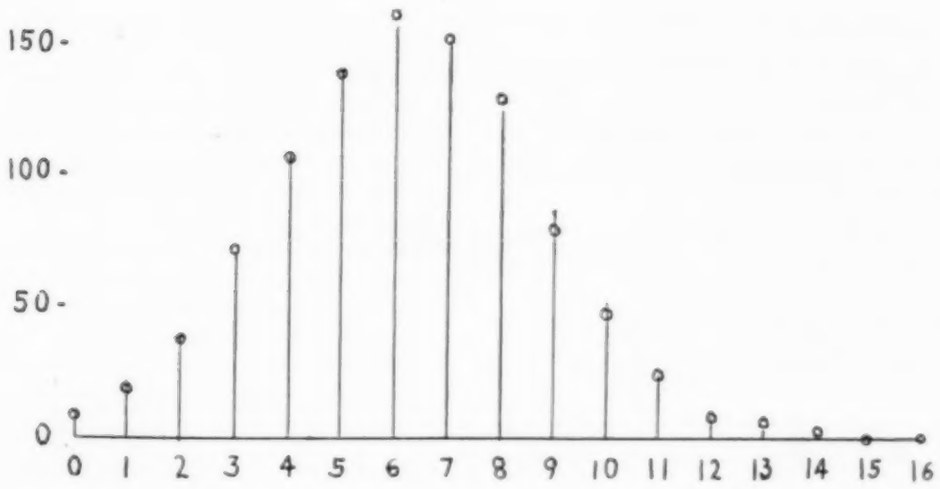


FIG. 2. The observed frequencies of each type of population according to number of aristapedia genes (small circles). These are compared with the theoretical frequencies in an array of populations in which a stable state has been reached with 86% selection against homozygous aristapedia, 60% against homozygous spineless, relative to heterozygotes, and with effective 2N of 10.7.

but not so decisively as to prevent the unfavorable allele from occasionally drifting into fixation against the pressure of selection. Those with aristapedia and spineless illustrate an approach to equilibrium between alleles because of selection against both homozygotes, but balancing of these selection pressures against random drift from inbreeding in such a way that gene frequency varies almost from one extreme to the other among the populations and one at least of the alleles may occasionally drift into fixation.

It should be recognized that in natural populations with effective size in the thousands, all other types of steady and random drift are likely to be present. Isolation from the rest of the species is not likely to be so complete that immigration can be neglected. Recurrent mutation may have to be considered. With respect to random drift it becomes necessary to take account of fluctuations in the coefficients pertaining to selection and amount and quality of immigration. In a broad sense, however, the experimental arrays may still be considered as exaggerated models of certain patterns of interplay of the directed and random processes which must be taken into account in the study of natural populations.

SUMMARY

Among 113 lines, each starting from four ss^a/ss females and four ss^a/ss males and continued to fixation or to ten generations by random selection of four females and four males in each generation, there was rapid attainment of a nearly stable distribution of gene frequencies. Spineless, however, drifted into fixation in eight lines. Aristapedia reached a maximum gene frequency of 87.5%. The mean gene frequency of aristapedia came to be 38.8%.

Analysis indicated very strong selection against both homozygotes in both viability and productivity. The viability coefficients were approximately in the ratio .50:1:.75 for ss^a/ss^a, ss^a/ss and ss/ss respectively with only slight differences in the sexes. The productivity coefficients were approximately in the ratio .40:1:.75 for these genotypes in females and 0:1:.25 in males.

A relatively simple empirical formula was obtained for the net rate of change of gene frequency per generation (net selective values in the ratio .14:1:.40). The observed distribution of gene frequencies agreed closely with that expected from those values among populations with effective $2N_e$ of 10.7.

Literature Cited

Kerr, W. E., and S. Wright. 1954. Experimental studies of the distribution of gene frequencies in very small populations of *Drosophila melanogaster*. I. Forked. Evolution **8**: 172–177.

Wright, S. 1937. The distribution of gene frequencies in populations. Proc. Nat. Acad. Sci., **23**: 307–320.

——. 1952. The genetics of quantitative variability. Quantitative Inheritance, p. 5–41, edited by E. C. R. Reeve and C. H. Waddington. London. 151 p.

Wright, S., and Th. Dobzhansky. 1946. Genetics of natural populations. XII. Experimental reproduction of some of the changes caused by natural selection in certain populations of *Drosophila pseudoobscura*. Genetics, **31**: 125–156.

Wright, S., and W. E. Kerr. 1954. Experimental studies of the distribution of gene frequencies in very small populations of *Drosophila melanogaster*. II. Bar. Evolution **8**: 225–240.

THE GENETIC POPULATION STRUCTURE OF BRAZILIAN *DROSOPHILA WILLISTONI* [1]

C. PAVAN AND E. N. KNAPP

Department of General Biology, University of São Paulo, Brazil

Received January 20, 1954

INTRODUCTION

Evolutionary processes which occur in a species are determined by the genetic nature of that species and by the environment in which it lives. As emphasized particularly by Wright (1931, 1948, 1951) no single cause (such as mutation, gene recombination, selection, genetic drift, or any one factor of the environment) is decisive in all evolutionary situations. It is rather the whole pattern of all these internal and external agents that is important, and these causal patterns vary from species to species. The recognition of the existence of a variety of evolutionary patterns in the living world is perhaps the outstanding difference between newer and older theories of evolution.

Nevertheless, quantitative estimates of even the most important genetic parameters are available for very few species. One of them is *Drosophila pseudoobscura*. Dobzhansky and Wright (1941, 1947) and Wright, Dobzhansky and Hovanitz (1942) have determined the magnitude of some of the variables for the populations of this species in some localities in California. The present article reports the results of similar analysis of Brazilian populations of *Drosophila willistoni*.

Drosophila willistoni and *D. pseudoobscura* are ecologically dominant species of Drosophila in their respective distribution areas (western North America for the former, American tropics for the latter). Nevertheless, it will be shown that the two species differ radically in their genetic structure. In *D. pseudoobscura* the populations studied have limited genetically effective sizes, as shown by the much higher frequencies of allelism between lethals derived from the same population than between lethals from different populations. In *D. willistoni*, the rates of allelism among lethals are in most cases independent of the geographic origin of the latter. This indicates that this species exists in populations which may be treated as having infinitely large effective sizes. Only the populations of *D. willistoni* coming from the small islands of Angra dos Reis have shown a high rate of allelism within populations. These island populations are, then, of limited genetically effective sizes.

THE POPULATION PARAMETERS

It is well known that natural populations of *Drosophila* and of other sexually reproducing and cross-fertilizing organisms carry great stores of concealed recessive genetic variants. In particular, many of the chromosomes in these populations are lethal in double dose, because of the occurrence in them of recessive mutant genes or lethal gene combinations. As shown by Wright, Dobzhansky, and others, the study of these recessive lethals may give some valuable information concerning the genetic population structure.

According to Wright (1943, 1948, and other works) the main population parameters are eight in number, namely:

N —genetically effective size of local populations
F —coefficient of inbreeding of these populations

[1] Contribution No. 14 of the cooperative research project of the University of São Paulo and Columbia University on genetics and ecology of tropical *Drosophila*.

m —coefficient of migration between the populations
n —number of loci in the chromosomes capable of giving rise to lethal mutations
$\bar{v}$ —mean mutation rate per locus giving rise to lethals
σ_v^2—variance of mutation rates giving rise to lethals
$\bar{s}$ —mean selection coefficient against heterozygous carriers of lethals
σ_s^2—variance of the selection coefficient against the heterozygous carriers of lethals.

A direct determination of all these population parameters has so far not been found feasible in any species. However, certain inferences concerning some of them are possible from primary data which are experimentally determined with varying degrees of precision. These primary data are as follows:

Q —the frequency in natural populations of chromosomes which are lethal when present in double dose,
V —the rate of origin of lethal chromosomes by mutation,
P_∞—the rate of allelism of independently arisen lethal chromosomes, and
P —the rate of allelism of lethal chromosomes within a local population.

The Frequencies of Lethal Chromosomes and Genes

Pavan *et al.* (1951) have analyzed 2,004 second chromosomes from populations of *D. willistoni* in twelve localities in tropical Brazil, and found 41.2±1.1 per cent of these chromosomes to be lethal or semilethal when homozygous (present in double dose). Later we analyzed 410 chromosomes from a thirteenth locality, Angra dos Reis, and found 42.7 per cent of them lethal or semilethal to homozygotes. In sum, 2,414 chromosomes were analyzed, and 41.5±1.0 per cent of them were lethal or semilethal. Different localities showed no striking heterogeneity with respect to the incidence of lethal chromosomes. However, Townsend (1952) and Cordeiro (quoted by Dobzhansky and Spassky, 1954) found that geographically submarginal populations of the same species in Florida and in southernmost Brazil, have somewhat lower frequencies of lethals (31.1±4.4 and 28.4+1.8 per cent respectively). Since the lethals tested in our experiments came from the same populations as those studied by Pavan *et al.*, we may take the value of Q to be equal for our purposes to 0.415±0.010.

The technique used for the detection of lethal chromosomes does not distinguish between chromosomes which have a single recessive lethal gene, and those having two or more such genes. The mean frequency of lethal genes per chromosome in the Brazilian populations may be determined by the formula (see Dobzhansky and Wright, 1941; Prout, 1954)

$$n\bar{q} = -\ln (1 - Q), \qquad (1)$$

where n is the number of loci in the second chromosome of *D. willistoni* which produce recessive lethals by mutation, $\bar{q}$ the mean frequency of lethals per locus in the population and ln the natural logarithms. The formula assumes that the numbers of lethals in the chromosomes in nature have a Poisson distribution. Using this formula, the $n\bar{q}$ value for our populations equals 0.536.

The Mutation Rate

Dobzhansky, Spassky, and Spassky (1952) have found that, in laboratory experiments, approximately 59 lethal and semilethal mutations have arisen in 6011 chromosome-generations analyzed. This indicates a mutation rate, V, in the second chromosomes of *D. willistoni* of approximately 0.00983, with 95 per cent confidence limits of 0.00760–0.01272.

TABLE 1.

LOCALITIES	VILA ATLANTICA	MOGI DAS CRUZES	PIRASSUNUNGA	ANGRA DOS REIS	GOIAS	CATUNI	PALMARES	JAPIIM	RIO MOA	CRUZEIRO DO SUL	BELEM	RIO NEGRO	MUCAJAI	LETHALS TESTED
VILA ATLANTICA	474													38
MOGI DAS CRUZES	316	787												46
PIRASSUNUNGA	90	132	1215											80
ANGRA DOS REIS	514	-	-	4227										109
GOIAS	21	40	12	-	1									2
CATUNI	440	550	173	1315	54	351								27
PALMARES	157	213	86	251	22	283	54							11
JAPIIM	80	91	24	-	8	130	44	8						5
RIO MOA	24	35	12	-	-	54	22	8	-					2
CRUZEIRO DO SUL	176	220	86	421	22	297	110	44	12	55				11
BELEM	28	40	12	-	4	54	22	8	2	22	1			2
RIO NEGRO	49	110	30	-	10	147	55	20	14	55	10	10		7
MUCAJAI	14	20	6	-	1	27	11	4	1	11	2	5	2	3
TOTAL INTRA	474	787	1215	1363	1	351	54	6	-	55	1	10	2	4319
TOTAL INTER	1887	1451	401	4851	121	992	264	84	29	88	12	5		10185
LETHALS TESTED														321

RATE OF ALLELISM OF INDEPENDENT LETHALS

Experiments were arranged to test the frequency of allelism between lethals from 13 different localities in various parts of Brazil (except the extreme south) listed in table 1. Of these localities, Vila Atlantica, Mogi das Cruzes, and Pirassununga are in the State of São Paulo, Angra dos Reis in the State of Rio de Janeiro; Goias (Fazenda Monjolinho) is a state in the central part of Brazil, Catuni in the State of Bahia, Fazenda Palmares, Japiim, Rio Moa, and Cruzeiro do Sul in the Territory of Acre, bordering Peru and Bolivia, Belem in the State of Para; Rio Negro refers to the banks of the river of this name northwest of Manaus in the State of Amazonas; and Mucajai is in the Territory of Rio Branco. The distances between these localities vary from about 20 miles (Japiim, Rio Moa) to hundreds and even thousands of miles. The natural migration rates of *D. willistoni* are so slow (Burla *et al.*, 1950) that we feel it safe to assume that the lethals found in the populations of different localities are independent in origin, i.e., that they are descended from different mutations. The lethals found within any one of the populations may, of course, be partly of independent origin and partly of common origin, descended from the same original mutant (Wright, Dobzhansky, and Hovanitz, 1942).

The conditions in one of the localities, namely Angra dos Reis, require further comments. Here the flies were collected on five different islands in the Bay of Angra dos Reis (see table 2). These islands vary in size from about 15 thousand square meters (Queimada Pequena) to about ten times this area (Emboassica). The distances between the islands on which collections were made vary from about 200 meters (Queimada Pequena to Queimada Grande) to several kilometers from each other and from the continent. In view of the relative smallness and the strong isolation of the populations of the different islands, we felt it possible to treat them as five separate localities, although they are, of course, much more nearly adjacent than any other localities in our material.

The lethals are perpetuated in balanced strains, the Star Hooked abbreviated brown Inversion chromosome acting as a balancer (see Pavan *et al.*, 1951). The allelism tests have been made by intercrossing different strains, and observing the presence or absence of wild-type (non-Star, non-Hooked) flies in the offspring. When many wild-type flies were present, no counts were made, and the lethals involved were scored as non-allelic. When no wild-type appeared, the cross was repeated three times, to exclude the possibility of experimental errors. No intermediate situations were observed, perhaps because only complete

TABLE 2.

ISLAND	QUEIMADA PEQUENA	QUEIMADA GRANDE	PAPAGAIOS	PORCOS	EMBOASSICA	LETHALS TESTED
QUEIMADA PEQUENA	529					35
QUEIMADA GRANDE	219	45				10
PAPAGAIOS	901	279	637			40
PORCOS	325	154	506	131		17
EMBOASSICA	189	69	113	109	21	7
TOTAL INTRA	529	45	637	131	21	1363
TOTAL INTER	1634	502	619	109		2864
LETHALS TESTED						109

TABLE 3. *Allelic lethals found among the intercrosses*

Intra-locality		Inter-locality	
Locality	Number of alleles	Locality	Number of alleles
Mogi	1	Vila Atlantica × Mogi	1
Catuni	1	Vila Atlantica × Pirassanunga	1
Pirassununga	3	Vila Atlantica × Angra	4
Angra (Within Islands)	7	Vila Atlantica × Palmares	1
		Mogi × Cruzeiro do Sul	1
		Mogi × Goias	1
		Mogi × Palmares	1
		Angra (Between Islands)	5
		Angra × Catuni	1
Total	12	Total	16

lethals and extreme semilethals were used. The numbers of the crosses examined are indicated in table 1. Not all the possible crosses between the lethals were made (with A lethals from one locality, and B lethals from another, AB crosses are possible). The total number of crosses between lethals from different localities is 10,185. This number includes the intercrosses of the lethals from the different islands of Angra dos Reis. (These intercrosses are shown in table 1 combined with the tests for allelism between lethals from the same island; the figure 4,227 intercrosses is, then, broken up in 1,363 intercrosses between lethals from the same island and 2,864 intercrosses between lethals from different islands, as shown in table 2.)

Table 3 lists the crosses between strains containing lethal chromosomes from different localities in which allelic lethals have been found. A total of 16 intercrosses among 10,185 contained allelic lethals. This gives the estimate of the value P_∞, the rate of allelism between independently arisen lethal chromosomes, of 0.00157. The 95 per cent confidence interval for this estimate is 0.00096 to 0.00258. Since a lethal chromosome may contain more than one lethal gene (see above), we may also calculate the value p_∞, the rate of allelism between independently arise lethal genes, according to the formula:

$$p_\infty = P_\infty(Q/n\bar{q})^2 = 0.00157 \times (0.415/0.536)^2 = 0.000941, \quad (2)$$

and the confidence intervals from 0.000632 to 0.001395 (Wright, Dobzhansky, Hovanitz, 1942).

RATE OF ALLELISM OF LETHALS FROM THE SAME POPULATION

As shown in table 1, a total of 4,319 intercrosses have been made between strains containing lethal chromosomes derived from flies collected in the same locality. This figure includes the 1,363 intercrosses between lethals from population samples taken within individual islands of Angra dos Reis. Since these island populations may not be comparable with populations on the continent (see above), they may be treated separately. Excluding them, we have 2,956 intercrosses between lethal chromosomes originating within a continental locality. As shown in table 3, five crosses have been found to contain allelic lethals within Mogi, Catuni, and Pirassanunga localities, and seven crosses with allelic lethals from Angra dos Reis. This yields an estimate of P, the rate of allelism of lethal chromosomes within a continental population, of 0.00169, and within a population of an island of Angra dos Reis of 0.00514. The 95 per cent confidence interval for continental

populations is from 0.00071 to 0.00402 and for the islands of Angra dos Reis from 0.00247 to 0.01070.

The rate of allelism between lethal genes from the same locality, p, may be computed as:

$$p = P - (P_\infty - p_\infty), \qquad (3)$$

which for continental populations gives the value 0.001061 (the confidence interval 0.00038–0.00285), and for the islands of Angra dos Reis 0.00451 (the confidence interval 0.00214–0.00952).

Comparison of Rates of Allelism of Lethals Within and Between Localities

Making all the allowances for the great experimental errors involved in the above estimates, certain conclusions from the data seem nevertheless justified. First, the frequency of allelism between lethals from the same continental population (0.001061) is not significantly different from that of the allelism of independently arisen lethals (0.000941). Second, the frequency of allelic lethals encountered within island populations in Angra dos Reis (0.00451) is higher than that for independently arisen lethals. (The respective confidence intervals are 0.00214–0.00952 and 0.000632–0.001395.) Thirdly, lethals from the island populations of Angra dos Reis are allelic probably more frequently than those within continental populations (the confidence intervals 0.00214–0.00952 and 0.000382–0.002835).

The situation observed in the Brazilian populations of *D. willistoni* differs profoundly from that observed by Wright, Dobzhansky, and Hovanitz (1942) in the California populations of *D. pseudoobscura*. In the latter populations, the frequency of alleles among lethals in the third chromosomes derived from flies collected at the same station (on Mount San Jacinto) is 0.0207, and at the same locality (in the Death Valley region) is 0.0305. The comparable rate of allelism of independently arisen lethals is, in *D. pseudoobscura*, 0.00345, or only about one-sixth to one-ninth of the allelism within a station or a locality, the difference being statistically quite significant. It may be pointed out in this connection that the territories of our "localities" within which the collections have been made in Brazil correspond fairly closely to the "stations" of Wright, Dobzhansky, and Hovanitz.

The difference found between the behaviors of the lethals in *D. willistoni* and *D. pseudoobscura* is indicative of an important dissimilarity of the genetic population structures in these two species. As shown by Wright (in Dobzhansky and Wright, 1941, 1947; Wright, Dobzhansky and Hovanitz, 1942, and elsewhere; see also Prout, 1954), the greater frequency of alleles among lethals from the same population than among independently arisen lethals is most likely due to restriction of the gentically effective size of the populations concerned. If this is the case, the genetically effective sizes of the continental populations of *D. willistoni* (the value N) are not distinguishable from infinite. On the other hand, the N's for the California populations of *D. pseudoobscura* and for the island populations of *D. willistoni* at Angra dos Reis are clearly limited. An attempt to assign a numerical value for the N at Angra dos Reis meets, however, with difficulty, as explained below.

The Problem of the Number of Mutable Loci in the Second Chromosome

As shown by Wright (in Dobzhansky and Wright, 1941; see also Prout, 1954), the number of loci in a chromosome which produce recessive lethals by mutation (n) is related to the frequency of allelism between independently arisen lethals (P_∞), the mean mutation rate per locus producing these lethals ($\bar{v}$), and the variance of mutation rates from locus to locus, together with that of selection rates against the heterozygotes ($\sigma^2_{q(D)}$) as

follows (Dobzhansky and Wright, 1941):

$$n = 1/p_\infty(1 + \sigma^2_{q(D)}/\bar{q}^2) \qquad (4)$$

Since the variance of the mutation and selection rates per locus is in practice not accessible for experimental determination, the improbable assumption is made that this variance is equal to zero. In this case the number of mutable loci may be estimated simply as:

$$n = 1/p_\infty \qquad (5)$$

but the figure obtained is certainly an underestimate. Using this formula, the n for the second chromosome of *D. willistoni* will be n = 1: 0.000945 = 1,063 with 95 per cent confidence limits of 717 to 1,582.

This estimate should be compared with that made by Wallace (1950) for the second chromosome of *D. melanogaster*, which is 400, with confidence limits 234–718. *D. willistoni* and *D. melanogaster* are fairly closely related species (belonging to the same subgenus), and their chromosomes are known to contain mostly the same loci (Spassky and Dobzhansky, 1950). The strikingly different estimates of the number of Mutable loci made by Wallace and by ourselves require an explanation. Although the confidence limits for the two estimates overlap slightly, the difference is unlikely to be due to sampling errors. Wallace's figure is based on studies of lethals induced by X-rays, and ours on work with naturally occurring lethals; this difference is, however, unimportant, since Ives (1945) found a frequency of alleles among independent naturally occurring lethals in *D. melanogaster* which is very close to that found by Wallace. Ives's figure leads to an estimate of n = 495, with confidence limits 285–705 (Wallace, 1950). The equation (4) shows that the observed difference between the n's might be accounted for if the group of lethals tested in *D. willistoni* were considerably less uniform than those in *D. melanogaster* (the variance, σ_v^2, greater in the former than in the latter species). There is, however, no obvious reason why this should be so.

We must face the possibility that there is a real difference in the n, the number of mutable loci, in the homologous chromosomes of the two species. Our arguments have, up to this point, been based on the implied assumption that the lethality of a chromosome in homozygotes is due to discrete mutant alleles, each of which causes death of the homozygotes regardless of the other genes in the same chromosome. Yet, Dobzhansky (1946) has been the first to discover the existence of so-called "synthetic lethals." Crossing-over between two chromosomes neither of which is lethal to homozygotes produces in *D. pseudoobscura*, some chromosomes which are lethal in double dose. Wallace *et al.* (1953) found the same to be the case in *D. melanogaster*. Dobzhansky worked with chromosomes derived from natural populations, while Wallace *et al.* dealt with chromosomes from laboratory x-rayed populations.

The phenomenon of "synthetic lethals" is still very little known, although it may prove to be quite important in populations of some species, including man. It is possible that lethals in Drosophila populations (and hereditary diseases in human populations) are of two kinds. First, there may occur mutations which produce alleles of certain loci which are always lethal to homozygotes, regardless of what other genes may be present in the same genotype. Secondly, there may exist alleles at some loci which are lethal only in combination with certain alleles at other loci. There is no need to suppose that the loci which produce the unconditional and the synthetic lethals are always distinct: some loci may mutate sometimes to alleles of the former and sometimes of the latter kind. The difference in n, the numbers of mutable loci, in the second chromosomes of *D. melanogaster* and *D. willistoni* may, then, be due to the inclusion of a greater number of synthetic lethals in the material studied

by ourselves than in that examined by Wallace (1950) and Ives (1945).

Because of the absence of data concerning the incidence of synthetic lethals in *D. willistoni* and *D. melanogaster*, estimates of the magnitude of the population numbers (N) became extremely difficult. Indeed, the value N is estimated from equations which include the quantities $\bar{\nu}$ and $\bar{q}$, the mean mutation rates per locus and the mean frequency of the lethals per locus in the populations concerned (Wright, Dobzhansky, and Hovanitz, 1942). The values $\bar{\nu}$ and $\bar{q}$ are estimated by dividing V and Q (the total mutation rate and the frequency of chromosomes which carry at least one lethal) by n, the number of loci which produce lethals. Very fortunately, this difficulty does not affect the estimate of N for the continental populations of *D. willistoni*. This is because the observed rates of allelism within and between continental populations are sensibly identical. Such identity means, regardless of the number of mutable loci involved, that the effective population size (N) is not distinguishable from infinity. The continental populations of *D. willistoni* in tropical Brazil have properties approaching those of ideal infinite populations.

A different situation obtains in the populations of the small islands in the bay of Angra dos Reis. Here the lethals collected within an island are allelic more frequently than are independently arisen lethals. Calculations made with different values on n (corresponding to the confidence limits 717 and 1582) have given figures for N in thousands.

Selection Against Heterozygotes Carrying Lethals

As indicated above, the average fitness of heterozygotes carrying a second chromosome which is lethal in double dose is lower than that of individuals free from such chromosomes. It should be emphasized that the average reduction of the fitness in heterozygotes for lethals does not preclude the existence of some lethals which are neutral or even heterotic in combination with certain chromosomes (Cordeiro and Dobzhansky, 1954). Prout (1952) has estimated the mean selection coefficient against the heterozygotes for lethals in natural populations of *D. willistoni* using Wright's formula:

$$\bar{S} = \frac{V - PQ^2(1 + V)}{Q(1 + 2V) - 2PQ^2(1 + V)} \qquad (6)$$

Prout's estimate of $\bar{S}$ is close to 0.020. Using the same formula, we obtain for the combined data from all the populations studied by ourselves the estimate of 0.0226, which is certainly not appreciably different from Prout's.

Discussion

Although only the orders of magnitude of some of the genetic parameters have been determined for Brazilian populations of *Drosophila willistoni*, these parameters give a rough idea about the genetic structure of these populations. It is interesting to consider this information against the background of what is known concerning the ecological properties of the species, and to compare the situation in *D. willistoni* with that in other species of Drosophila.

D. willistoni is the commonest, or one of the commonest, species of Drosophila in most parts of tropical Brazil. Furthermore, it occurs in a great variety of habitats—from equatorial and coastal rain forests to gallery forests and savannas of the interior, and even to the deserts (caatingas) of the northeastern part of the country. The adults are attracted to many kinds of fermenting fruits and other carbohydrate-rich substances. Little is known about the food of the larvae but it is likely that they may develop in many, if not in all, places which attract the adults. In some localities the populations undergo pronounced seasonal expansions and contractions, while in other localities the populations seem to remain large and actively breed-

ing throughout the year (Dobzhansky and Pavan, 1950; Pavan, 1952).

Being a common, ubiquitous, and ecologically very versatile species, the local populations of *D. willistoni* show the genetic properties indistinguishable from those expected in ideal populations of infinite effective size. In such species, all populations will carry most of the possible mutant alleles of all genes, with frequencies determined by their mutation rates and selection coefficients. The frequencies of alleles between mutants found in natural populations should, then, be independent of the geographic origin of these populations. This is exactly what is indicated by our data, except for the Angra dos Reis populations. It is interesting that the California populations of *D. pseudoobscura* studied by Dobzhansky and Wright show significantly higher frequencies of alleles between mutants found within a population than between those found in geographically remote populations. *D. pseudoobscura* is an ecologically dominant species in western United States, but the effective sizes of its populations are evidently smaller than in *D. willistoni*, and this despite the fact that the migration rates (the value m, see above) are appreciably greater in *D. pseudoobscura* (Dobzhansky and Wright, 1947) than in *D. willistoni* (Burla *et al.*, 1950). The explanation is probably that the populations of *D. pseudoobscura* are subject to much greater seasonal expansions and contractions than those of tropical species like *D. willistoni*, at least in many of the localities inhabited by the latter.

Another property of *D. willistoni* is the presence in its populations of great stores of genetic variability, both concerning the structure of its chromosomes and of its genes. In this respect *D. willistoni* exceeds its close relatives in the tropics—*D. paulistorum*, *D. tropicalis*, and *D. equinoxialis*, which are less common and ecologically less versatile (Dobzhansky, Burla, and da Cunha, 1950); it also exceeds the temperate *D. pseudoobscura*, which is comparable to *D. willistoni* in ecological dominance. Comparison of the mutation rates in the homologous chromosomes suggests that *D. willistoni* is also more mutable than *D. pseudoobscura*, *D. melanogaster*, and the rare species *D. prosaltans* which is sympatric with *D. willistoni* (Dobzhansky, Spassky, and Spassky, 1952). Whether this higher mutability characterizes the chromosomes as wholes, or also separate gene loci in these chromosomes, is uncertain in view of the divergent estimates of the numbers of mutable loci in apparently homologous chromosomes (see above).

Taken as whole, the genetic system found in *D. willistoni* may, perhaps, prove to be characteristic of ecologically successful, biotically versatile species, which form large interbreeding populations.

Summary

Samples of natural populations of *Drosophila willistoni* were collected in various parts of Brazil. Among the 2,414 second chromosomes from these samples which were tested for viability effects in homozygous condition, 41.5± 0.1 per cent proved lethal or semilethal to homozygotes. Strains containing 321 of these lethal or extreme semilethal chromosomes from 13 different localities were intercrossed in order to test which of these lethals were allelic. In 10,185 intercrosses the lethal chromosomes were derived from populations of remote localities; in 16 of these intercrosses the lethals were allelic. The rate of allelism between lethals of independent origin is, therefore, 0.00157. In 2,956 intercrosses the pairs of lethal chromosomes were derived from the same locality; in 5 of them the lethals were alleles. The rate of allelism between geographically related lethals is, then, 0.00169. Only the lethals found in the populations of small isolated islands of Angra dos Reis were alleles somewhat more frequently: 7 alleles in 1,363 intercrosses, or a rate of 0.00514.

From the rate of allelism of independently arisen lethals, the number of gene loci in the second chromosome of *D. willistoni* can be estimated to be at least 1,063. This is more than double the estimate of the corresponding number in the second chromosome of *D. melanogaster* made by Wallace. And yet, the second chromosomes of these two species have been shown by Spassky and Dobzhansky to carry mostly the same loci. One of the possible reasons of the discrepancy may be that some of the lethals in the chromosomes of natural populations of *D. willistoni* are "synthetic," i.e., due to linkage of two or more loci neither of which is lethal by itself. Although the possibility of the occurrence of synthetic lethals introduces an element of ambiguity in calculation of certain genetic population parameters, the fact that the rates of allelism of lethals are independent of the geographic origin of the latter (except in the islands of Angra dos Reis) is very significant. It shows that the genetic structure of Brazilian populations of *D. willistoni* approaches that of ideal populations of infinite effective size. In this respect *D. willistoni* differs greatly from the California populations of *D. pseudoobscura* which have been shown by Wright and Dobzhansky to be of limited genetically effective sizes.

Acknowledgments

The Rockefeller Foundation and the Brazilian National Research Council (Conselho Nacional de Pesquizas) have contributed the grants which have made the present work possible. The authors take pleasure in expressing their obligations to Professor Theodosius Dobzhansky for his interest and advice on the work and for help in the preparation of the manuscript; to Professor Sewall Wright and to Mr. R. Lewontin for advice concerning the treatment of the data; and to Mrs. M. L. Pavan, Mr. L. E. Magalhães and Mr. Juan Nacrur for assistance in making some of the numerous crosses the results of which are described in the present article.

Literature Cited

Burla, H., A. B. da Cunha, A. G. L. Cavalcanti, Th. Dobzhansky, and C. Pavan. 1950. Population density and dispersal rates in Brazilian *Drosophila willistoni*. Ecology, **31**: 393–404.

Cordeiro, A. R., and Th. Dobzhansky. 1954. Combining ability of certain chromosomes in *Drosophila willistoni* and invalidation of the "wild-type" concept. Amer. Naturalist (in press).

Dobzhansky, Th. 1946. Genetics of natural populations. XIII. Recombination and variability in populations of *Drosophila pseudoobscura*. Genetics, **31**: 269–290.

Dobzhansky, Th., H. Burla, and A. B. da Cunha. 1950. A comparative study of chromosomal polymorphism in sibling species of the *willistoni* group of Drosophila. Am. Nat., **84**, 229–246.

Dobzhansky, Th., and C. Pavan. 1950. Local and seasonal variations in relative frequencies of species of Drosophila in Brazil. J. Anim. Ecol., **19**: 1–14.

Dobzhansky, Th., and B. Spassky. 1954. Genetics of natural populations. XXII. A comparison of the concealed variability in *Drosophila prosaltans* with that in other species. Genetics (in press).

Dobzhansky, Th., B. Spassky, and N. Spassky. 1952. A comparative study of mutation rates in two ecologically diverse species of Drosophila. Genetics **37**: 650–664.

Dobzhansky, Th., and S. Wright. 1941. Genetics of natural populations. V. Relation between mutation rates and accumulation of lethals in populations of *Drosophila pseudoobscura*. Genetics, **26**: 23–51.

———. 1947. Genetics of natural populations. XV. Rate of diffusion of a mutant gene through a population of *Drosophila pseudoobscura*. Genetics, **32**: 302–324.

Ives, P. T. 1945. The genetic structure of American populations of *Drosophila melanogaster*. Genetics, **30**: 167 196.

Pavan, C. 1952. Relacões entre populacoes naturais de Drosophila e o meio ambiente. Tese de Faculdade de Filosofia Ciencias e Letras da Universidade de São Paulo, Brasil.

Pavan, C., A. R. Cordeiro, N. Dobzhansky, Th. Dobzhansky, C. Malogolowkin, B. Spassky, and M. Wedel. 1951. Concealed genic variability in Brazilian populations of *Drosophila willistoni*. Genetics, **36**: 13–30.

Prout, T. 1952. Selection against heterozygotes for autosomal lethals in natural populations of *Drosophila willistoni*. Proc. Nat. Acad. Sci., **38**: 478–481.

——. 1954. Genetic drift in irradiated experimental populations of *Drosophila melanogaster*. Genetics (in press).

SPASSKY, B., AND TH. DOBZHANSKY. 1950. Comparative genetics of *Drosophila willistoni*. Heredity, **4**: 201–215.

TOWNSEND, J. IVES, JR. 1952. Genetics of marginal populations of *Drosophila willistoni*. Evolution, **6**: 428–442.

WALLACE, B. 1950. Allelism of second chromosome lethals in *Drosophila melanogaster*. Proc. Nat. Acad. Sci. **36**: 654–657.

WALLACE, B., J. C. KING, C. V. MADDEN, B. KAUFMANN, AND E. C. MCGUNNIGLE. 1953. An analysis of variability arising through recombination. Genetics, **38**: 272–307.

WRIGHT, W. 1931. Evolution in Mendelian populations. Genetics, **16**: 98–159.

——. 1943. Isolation by distance. Genetics, **28**: 114–138.

——. 1948. On the roles of direct and random changes in genes frequency in the genetics of population. Evolution, **2**: 279–294.

——. 1951. Fisher and Ford on "The Sewall Wright Effect." American Scientist, **39**: 452–479.

——, TH. DOBZHANSKY, AND W. HOVANITZ. 1942. Genetics of natural populations. VII. The allelism of lethals in the third chromosome of *Drosophila pseudoobscura*. Genetics, **27**: 363–394.

NATURAL HYBRIDIZATION IN THE *PEROMYSCUS LEUCOPUS* SPECIES GROUP OF MICE[1]

W. H. McCarley

Stephen F. Austin State College, Nacogdoches, Texas

Received Feb. 8, 1954

Introduction

The *Peromyscus leucopus* species group includes two species, the wood-mouse (*Peromyscus leucopus*) and the cotton-mouse (*P. gossypinus*) (Osgood, 1909). Both species are inhabitants of forested areas in the eastern part of the United States and in part of the Mississippi Valley the geographic ranges of the two species overlap broadly. Where these two sympatric species occur together, *leucopus* is generally restricted to the uplands and *gossypinus* occurs predominantly in the lowlands (Howell, 1921; McCarley, 1954). Occasionally, however, their ecologic distribution may overlap (Calhoun, 1941; McCarley, *op. cit.*)

The potentialities for natural hybridization have been shown to exist in all vertebrate groups that have been adequately studied (Blair, 1951). In nature there apparently are certain isolating factors that tend to keep a considerable number of sympatric species separate and distinct. These isolating factors and their effect on natural populations have been pointed out by Mayr (1942), Blair (1951), and others. It seems to be true that populations of animals usually acquire mechanisms of reproductive isolation before they have diverged genetically to the point of intersterility (Blair, *op. cit.*). With the exception of the birds there are comparatively few reports of interspecific hybridization in nature in the vertebrate groups. Only one presumed interspecific hybrid combination has been reported from nature in the genus *Peromyscus*. Four presumed hybrids between *leucopus* and *gossypinus* have been reported from Alabama by Howell (1921).

Dice (1937, 1940) demonstrated that there is apparently complete interfertility between *Peromyscus leucopus* and *P. gossypinus*. Dice (1940) was also able to demonstrate that the offspring from these various interspecies crosses are fully interfertile, both with each other and when backcrossed to the parent stocks.

Because the *leucopus* group is potentially capable of producing interspecific hybrids (at least in the laboratory), a critical analysis was undertaken of available specimens from the zone where the geographic ranges of the two species overlapped. For this purpose 415 specimens were available from the following sources: Museum of Zoology, Louisiana State University; U. S. Fish and Wildlife Service; Department of Wildlife Management, Texas A. and M. College; Texas Natural History Collection, University of Texas; and specimens which I had collected. These 415 specimens were studied with the primary purpose of learning whether natural hybridization did or did not occur in the *Peromyscus leucopus* species group. Because only adult specimens were utilized in this study only part of the 415 available specimens could be fully utilized (see table 1).

I wish to thank Dr. W. F. Blair for advice during the course of this study and for critically reading the manuscript. I am grateful to Mr. W. N. Bradshaw, Dr. W. A. Thornton, and Mr. W. V. Robertson for assistance with the field work. I wish to thank Mr. Philip McCarley for aid in preparation of the illustrations and Dr. W. B. Davis, Dr. H. H.

[1] Presented as a portion of a doctoral dissertation at the University of Texas.

T. Jackson and Dr. George Lowery for loaning specimens for study.

As has been pointed out earlier (Osgood, 1909; Dice, 1940), the only obvious morphological distinction between the species *leucopus* and *gossypinus* is that the latter is decidedly the larger. Because these two species are widely distributed and occupy somewhat diverse areas there is a considerable amount of geographic variation in their morphological characters. As a result of the morphological variation within each of the two species, there are no clear cut qualitative differences than can be used to definitely separate the two species (Dice, 1940). The most useful character for distinguishing between the two species appears to be length of the hind foot. The cotton-mouse nearly always has a much larger hind foot than does the wood-mouse. There is an overlap of this character over the entire geographic range of the two species, but it has been found that as a rule the length of the hind foot does not overlap in a given area. This situation was also the case for the *leucopus* and *gossypinus* examined by Dice (1940) from the Dismal Swamp region of Virginia. There are apparently no other consistent differences between the two species in morphological characters.

The following discussion of hybridization is based on certain morphological characters. In all of the individuals that were examined, the following standard measurements were obtained: length of body, length of tail, length of hind foot, length of ear (in part), greatest length of skull, narrowest width of interorbital constriction, length of diastema, greatest length of maxillary tooth row, and greatest length of auditory bulla. The external measurements that are used were taken from the museum tags on the specimens. These latter measurements are subject to some error because they were made by various individuals, including students who were not experienced in measuring and preparing study skins. In the opinion of the author some of the external measurements were in error, and when such appeared to be obviously the case, these measurements were not included in the analysis.

Dice (1940) found that the offspring of laboratory crosses between *leucopus* and *gossypinus* were intermediate in morphological characters between the parent stocks. This intermediacy in morphological characters was used as the criterion in the present study to distinguish between suspected hybrids and the remainder of the individuals in the populations.

In the attempt to systematically analyze the populations, it was found that certain characters were of more value in separating the two species than were other characters. Those characters which appeared to be of the most value are as follows, listed in the order of their decreasing importance: length of hind foot, length of skull, body length, length of diastema, length of auditory bullae, and length of maxillary tooth row. In order to show these characters graphically, pictorialized scatter diagrams (figs. 1–3) as proposed by Anderson (1949) were used.

Individuals were plotted on these diagrams according to the following system. The vertical coordinate represents length of hind foot and the horizontal coordinate represents length of skull. The blackened circles thus represent the position of individual mice according to the length of hind foot and length of skull. The spikes on the circles represent four additional morphological characters. These spikes are drawn to scale and are either two, four, six or eight millimeters long. The spike located at the twelve o'clock position represents body length. The absence of a spike at this position indicates that the body length was between 70 and 79 mm. A spike 2 mm. long represents a body length of between 80 and 89 mm. and for every 10 mm. increase in body length there is a corresponding 2 mm. increase in spike length. The spike at the three o'clock position represents the length of the maxillary tooth row. No spike rep-

TABLE 1. *The number of specimens, the average measurements and the extreme measurements of the morphological characters of the adult specimens of* Peromycus leucopus *and* P. gossypinus *from each species population*

Locality	Body length	Tail length	Foot length	Skull length	Interorb. const.	Diastema	Max. tooth row	Aud. bulla
Anderson Co., Tex.								
leucopus	4(90.0)83–98	4(68.0)63–73	4(20.0)19.4–20.5	4(26.1)25.3–27.2	4(4.2)4.1–4.5	4(6.6)6.5–6.8	4(3.6)3.5–3.7	4(4.5)4.1–4.6
gossypinus	12(100.0)86–100	12(75.6)71–85	12(22.7)22.0–23.8	11(28.3)26.4–30.6	11(4.4)4.2–4.8	11(7.4)6.6–8.1	11(3.6)3.4–3.8	10(4.8)4.7–5.1
Brazos Co., Tex.								
leucopus	16(88.8)76–103	16(65.6)55–75	16(19.8)19.0–21.0	16(25.6)24.1–27.3	16(4.2)3.9–4.4	16(6.5)6.0–7.0	15(3.4)3.1–3.7	14(4.5)4.2–5.1
gossypinus	2(111.0)107–114	2(83.0)80–86	2(25.0)24.0–26.0	2(29.3)28.6–30.0	2(4.6)4.5–4.7	2(7.6)7.5–7.6	2(3.8)3.7–3.9	2(5.1)4.9–5.2
Cherokee Co., Tex.								
gossypinus	13(99.0)85–111	13(72.0)65–78	13(22.5)21.0–25.0	10(28.7)27.3–30.8	13(4.5)4.3–4.7	12(7.4)6.9–8.2	13(3.7)3.5–3.9	13(5.2)4.9–5.9
Harrison Co., Tex.								
leucopus	4(88.0)80–92	4(61.0)56–64	3(18.7)18.5–18.8	4(24.8)23.8–25.2	4(4.0)3.9–4.2	4(6.1)5.9–6.5	4(3.6)3.4–3.7	4(4.5)4.2–4.9
gossypinus	6(100.0)94–103	6(72.0)62–83	6(23.0)22.0–23.5	6(28.2)26.8–29.2	6(4.3)4.0–4.6	6(7.1)6.0–7.7	6(3.7)3.4–3.8	6(5.2)4.9–5.4
Henderson Co., Tex.								
leucopus	14(87.6)77–98	14(62.9)53–76	14(20.0)19.4–21.0	14(25.1)23.7–26.6	14(4.3)3.9–4.6	14(6.4)5.9–6.8	14(3.5)3.2–3.7	14(4.5)4.1–5.0
gossypinus	18(103.0)91–110	18(71.0)55–80	18(22.4)21.8–23.0	15(28.2)26.9–29.6	15(4.6)4.2–4.9	15(7.2)6.7–8.5	15(3.7)3.5–3.8	15(5.0)4.4–5.6
Nacogdoches Co., Tex.								
leucopus	1(83.0)	1(59.0)	1(19.2)	1(25.1)	1(4.1)	1(6.4)	1(3.7)	1(4.3)
gossypinus	47(104.1)80–113	44(75.6)62–91	47(23.1)21.8–24.8	44(28.9)26.5–31.1	46(4.6)4.0–4.9	46(7.6)6.9–8.5	46(3.9)3.5–4.0	43(5.2)4.1–5.8
Newton Co., Tex.								
leucopus	12(93.0)83–102	12(67.8)56–76	12(19.9)18.5–21.2	12(26.1)23.9–27.3	12(4.3)4.0–4.6	12(6.6)6.0–7.2	12(3.5)3.2–3.9	12(4.6)4.0–5.1
gossypinus	6(101.2)96–105	6(83.0)77–88	6(23.7)22.9–23.9	6(29.1)28.0–30.2	6(4.5)4.4–5.0	6(7.6)7.1–8.1	6(3.7)3.3–3.9	6(5.1)4.8–5.4
Polk Co., Tex.								
gossypinus	13(100.0)80–116	13(78.0)70–88	13(23.1)22.0–25.2	13(29.0)27.9–30.6	13(4.7)4.4–4.9	13(7.4)6.9–7.9	13(3.7)3.5–4.0	12(5.1)4.9–5.3

TABLE 1.—*Continued*

Locality	Body length	Tail length	Foot length	Skull length	Interorb. const.	Diastema	Max. tooth row	Aud. bulla
Central Alabama								
leucopus	2(107.0)106–108	2(64.0)62–66	2(19.5)19.0–20.0	2(26.0)25.8–26.3	2(4.4)4.3–4.4	2(6.7)6.5–6.9	2(3.4)3.4–3.5	2(4.3)4.2–4.4
gossypinus	6(107.0)93–116	6(75.0)63–82	6(23.6)23.0–24.0	6(28.9)26.8–30.5	6(4.6)4.4–4.8	6(7.5)6.7–8.2	6(3.8)3.7–3.9	6(4.8)4.6–5.0
Eastern Alabama								
leucopus	2(91.0)85–97	2(61.0)56–66	2(19.0)19.0	2(25.8)25.5–26.2	1(4.2)	2(6.3)6.0–6.5	2(3.6)3.6–3.7	1(4.6)
gossypinus	9(105.0)100–113	9(78.0)71–88	9(22.4)21.0–23.5	9(28.3)26.7–30.0	9(4.4)4.1–4.7	8(7.2)6.9–7.5	8(3.8)3.6–4.1	8(4.8)4.7–5.2
Northeastern Alabama								
leucopus	5(90.0)87–95	5(62.0)63–77	5(19.5)19.0–20.0	5(25.0)24.4–25.5	5(4.1)4.0–4.4	5(6.5)6.1–6.7	5(3.5)3.3–3.5	5(4.3)4.0–4.6
gossypinus	11(106.0)102–109	11(81.0)73–88	11(22.7)21.0–24.0	11(28.9)27.0–30.0	11(4.5)4.4–4.7	11(7.4)6.9–8.1	11(3.9)3.7–4.1	11(4.8)4.3–5.0
Northwestern Alabama								
leucopus	1(98.0)	1(65.0)	1(20.0)	1(25.4)	1(4.5)	1(6.7)	1(3.4)	1(4.0)
gossypinus	7(103.0)94–106	7(75.0)71–78	7(23.0)22.0–23.5	7(28.1)26.7–29.0	7(4.5)4.1–4.7	7(7.2)7.0–7.5	7(3.8)3.6–4.1	7(4.7)4.4–5.0
Western Alabama								
gossypinus	9(100.0)93–113	9(79.0)77–84	9(22.8)22.0–24.0	8(17.9)28.1–30.1	8(4.5)4.4–4.7	6(7.4)7.1–7.8	6(3.8)3.7–4.1	8(4.9)4.6–5.2
Northwestern Louisiana								
leucopus	2(83.0)82–84	2(64.0)60–68	2(19.5)19.0–20.0	1(26.1)	1(4.2)	1(6.8)	1(3.7)	1(4.7)
gossypinus	15(101.0)84–110	15(73.0)60–86	15(23.0)22.0–25.0	11(28.9)27.2–30.6	8(4.5)4.2–4.8	9(7.4)6.8–8.0	10(3.8)3.6–4.1	9(4.9)4.7–5.5
Southeastern Louisiana								
leucopus	9(88.0)79–100	9(66.0)55–80	9(19.8)18.0–20.6	9(26.0)24.8–27.5	9(4.4)3.9–4.7	9(6.9)6.0–7.1	9(3.7)3.5–4.2	9(4.6)4.0–4.7
gossypinus	44(93.5)81–113	42(76.0)65–89	43(22.8)21.7–24.7	41(28.7)25.8–30.3	44(4.5)4.2–4.8	42(7.2)6.3–8.0	43(3.6)3.5–4.1	42(4.9)4.3–5.3
Bryan Co., Oklahoma								
leucopus	17(85.0)79–90	16(64.0)56–68	17(19.2)17.7–20.0	14(25.9)24.4–26.8	15(4.2)4.0–4.5	15(6.6)6.0–6.9	15(3.5)3.4–3.7	15(4.5)4.0–5.0

resents a tooth row length of between 2.5 and 2.9 mm. and for every 0.5 mm. increase in tooth row length there is a corresponding 2 mm. increase in spike length. The spike at the six o'clock position represents the length of the diastema. No spike represents a diastema of 5.5 to 5.9 mm. in length and for every 0.5 mm. increase in diastema length there is a corresponding 2 mm. increase in spike length. The spike at the nine o'clock position represents the greatest length of the auditory bulla. No spike indicates that the bullar length was less than 4.0 mm. and for every 0.5 mm. increase in bullar length there is a corresponding 2 mm. increase in spike length. In some cases the above measurements were missing from the tag or the skull was broken in such a manner that the measurement in question could not be made. In these cases there is a small dot opposite the position of the spike to indicate the omission of that particular character.

Because individuals of the species *gossypinus* generally have larger hind feet and longer skulls than do members of the species *leucopus,* we would expect those individuals belonging to the species *gossypinus* to fall in the upper right of the scatter diagrams. It would further be expected that those individuals falling in this part of the diagram would exhibit the largest morphological characters as represented by the spikes. On the other hand, we would expect the smallest individuals, or those individuals belonging to the species *leucopus,* to fall in the lower left of the diagram. It would follow then that these individuals would exhibit the smallest morphological characters as represented by the spikes. Because Dice (1940) found that hybrids between *leucopus* and *gossypinus* were intermediate in morphological characters, we would expect any hybrids, if present, to occur on the diagrams between the individuals representing the species *leucopus* and *gossypinus.* Specimens have been examined from 51 localities in Alabama, Louisiana, Oklahoma, and Texas. In order to have as large a series as possible from one area, the specimens were arranged according to the regions (table 1), from which they were obtained. This somewhat arbitrary grouping used, as far as possible, any natural or ecologic boundaries that might exist. The distribution of the individuals in these populations has been plotted on scatter diagrams. These diagrams show the morphologic relationships in respect to interspecific hybridization that existed in the populations of *leucopus* and *gossypinus.*

Data

Three general kinds of morphologic relationships are found to exist in the populations. These morphologic relations are: (1) no apparent hybridization between *leucopus* and *gossypinus,* (2) occasional interspecific hybridization between the two species, (3) frequent interspecific hybridization between the two species. The three populations considered below represent these three types of morphologic relationships.

The relationship in which the populations showed no evidence of hybridization is typified by a sample of 12 *leucopus* and six *gossypinus* from a population located 15 miles east of Buna, Newton County, Texas and is represented in figure 1. It can be seen (fig. 1) that there are fairly distinct morphological differences between the two species in this region. There is an overlap of some of the morphologic characters but this degree of overlap also exists in populations of *leucopus* and *gossypinus* that are geographically isolated from each other. (For example, see Bryan County, Oklahoma *leucopus* and Polk County, Texas *gossypinus* (table 1).) In spite of this overlap of some of the characters, there are two well defined groups as illustrated by figure 1 and none of the individuals represented in this figure appear to be intermediates. All of the specimens are readily referable either to the species *leucopus* or to the species *gossypinus.* Apparently in this region there has been no interspecific hybridiza-

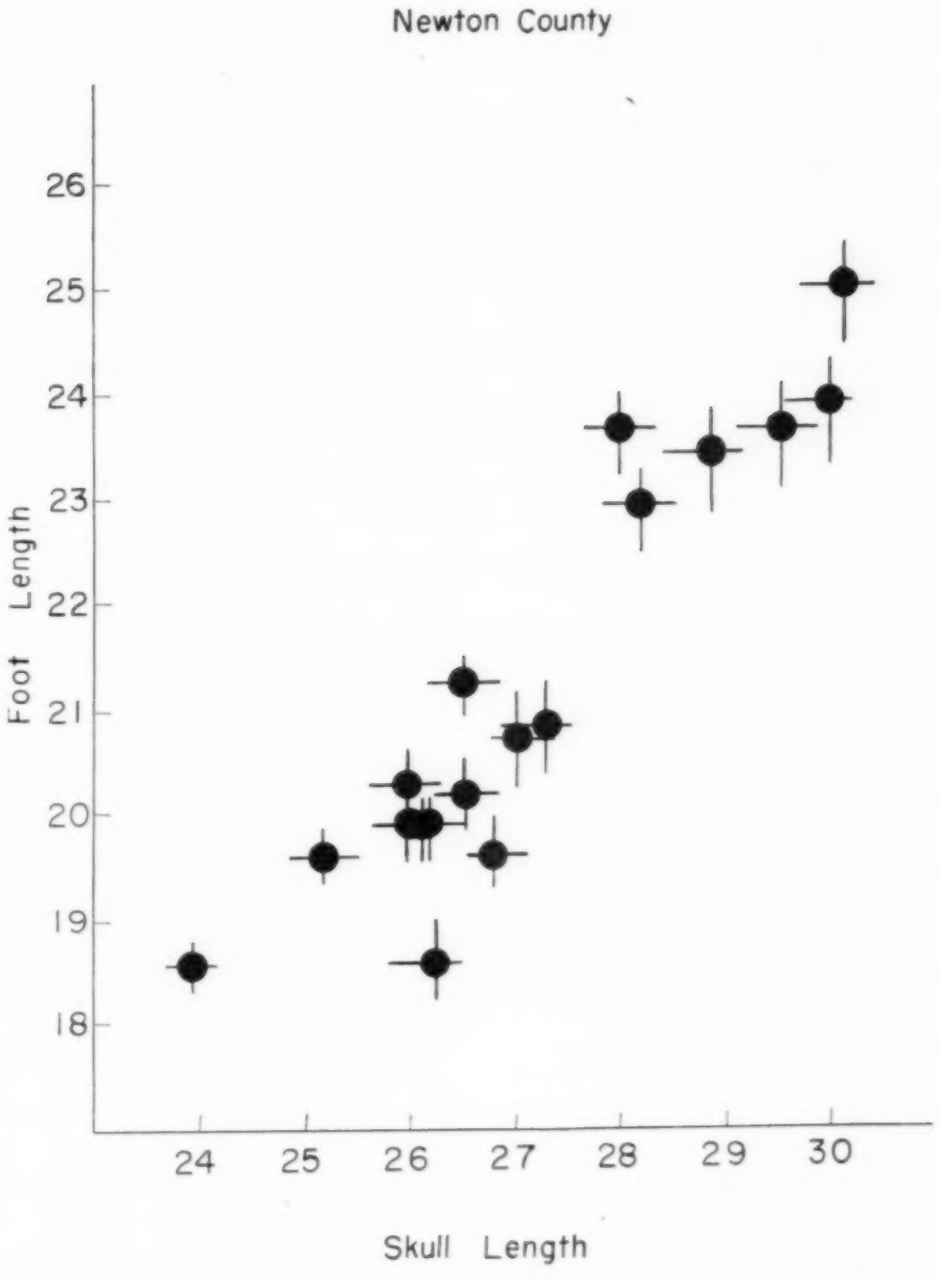


FIG. 1. The morphological relationship of a sample of *Peromyscus leucopus* and *P. gossypinus* collected 15 miles east of Buna, Newton County, Texas. (For explanation of figure, see text, page 318.)

tion of sufficient frequency to show in the sample and consequently the two populations are morphologically distinct. Similar relationships were found in populations from Brazos County, Cherokee County, Harrison County, and Polk County, Texas, and northeastern Alabama, northwestern Alabama, and northwestern Louisiana.

The second relationship in which there was evidence of occasional hybridization is exhibited by a sample of 14 *leucopus* and 15 *gossypinus* from the vicinity of Malakoff, Henderson County, Texas and is represented in figure 2. The majority of the individuals that are portrayed on figure 2 are definitely members of the species *leucopus* or *gossypinus*. One specimen, indicated on figure 2 by the letter H, is intermediate in the majority of its morphological characters and is not definitely referable to either species. This

individual is considered to be a natural hybrid between *leucopus* and *gossypinus*. This specimen (No. 2990, Table 2) is now in the University of Texas Natural History Collection. It would appear that in the populations of *leucopus* and *gossypinus* in Henderson County, there has been only occasional interspecific hybridization. This is indicated by the fact that the over-all morphological differences between the species populations in Henderson County are, on the average, only slightly less than the differences between the species populations in Newton County and other populations which did not appear to have hybridized. It would seem that if interspecific hybridization had been widespread in Henderson County, there would have been less of a morphologic difference between populations of the two species. This condition would have resulted from the exchange of genes between the two species populations as a result of backcrossing of hybrid individ-

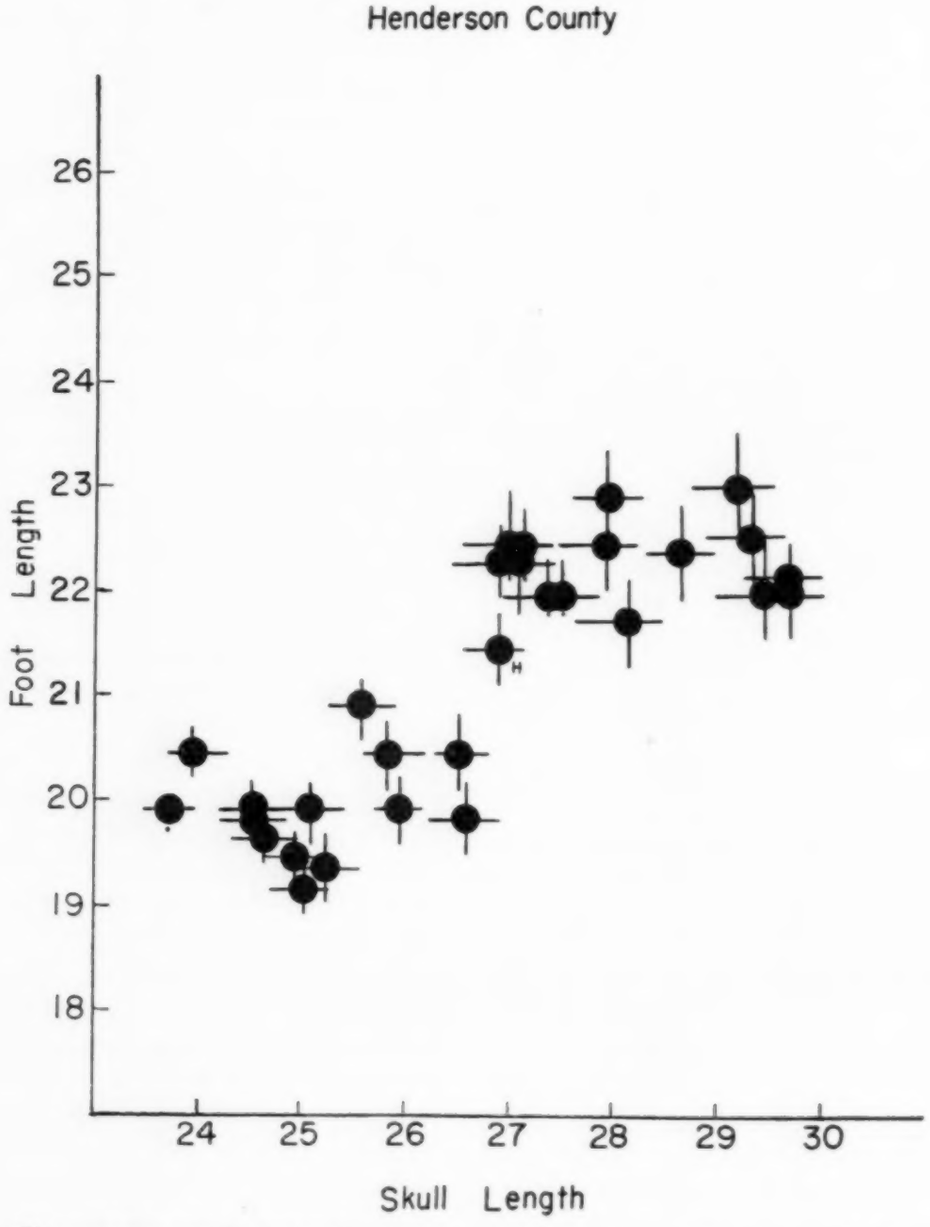


FIG. 2. The morphological relationship of a sample of *Peromys us leucopus* and *P. gossypinus* collected from the vicinity of Malakoff, Henderson County, Texas. The individual indicated by the letter H is considered a natural hybrid between the two species. (For explanation of figure, see text, page 319.)

TABLE 2. *The measurements of the morphological characters of natural hybrids between* Peromyscus leucopus *and* P. gossypinus

Museum number	Body length	Tail length	Foot length	Skull length	Interorb. const.	Diastema	Max. tooth row	Aud. bulla
TNHC								
2989	98	78	21.7	25.5	4.3	6.5	3.7	5.3
2990	98	65	21.5	26.9	4.2	7.3	3.4	4.9
USNM								
178357	100	72	22.0	26.7	4.5	6.9	3.7	4.9
178461	100	70	21.0	26.4	4.4	6.9	3.6	4.7
207285	99	69	21.0	28.2	4.3	7.0	3.8	4.9
211505	93	63	21.0	28.1	4.5	6.9	3.8	4.8
LSUMZ								
1628	92	82	21.0	28.1	4.2	7.5	3.7	4.5
2380	86	67	21.0	26.1	4.5	6.9	3.7	5.0
3502	100	72	21.0	27.6	4.6	6.9	3.6	4.7

uals with one or the other of the parent species. This backcrossing would have tended to obliterate species differences between the populations. This is apparently not the case that exists at present in populations of *leucopus* and *gossypinus* in Henderson County. Similar relationships were exhibited by populations from Anderson County (no actual hybrids) and Nacogdoches County, Texas, central Alabama, eastern Alabama, and western Alabama.

The third relationship in which there appears to have been frequent hybridization is exhibited by specimens from several localities in southeastern Louisiana, largely from the vicinity of Baton Rouge, and is shown in figure 3. It is obvious from the distribution of the individuals in figure 3 that there is no distinct morphological separation of the two species in this region. There is a considerable overlap of all morphological characters with the exception of the hind foot length (table 1). Nine individuals of this series are clearly referable to the species *leucopus* and 34 individuals are referable to the species *gossypinus*. Three individuals, which are indicated on figure 3 by the letter H, are intermediate in most of their morphologic characters and are not clearly referable to either species. I would consider these three individuals (Louisiana State University, Museum of Zoology, Numbers 2380, 1628, 3502—table 2) to be natural hybrids between *leucopus* and *gossypinus*. The one remaining individual with a foot length of 21 mm. is questionable but falls closest to the species *gossypinus*. This individual (L. S. U. M. Z., No. 2567) is not considered here to be an F_1 hybrid between *leucopus* and *gossypinus*, but it is quite possible that this specimen represents the offspring of a backcross of an individual of hybrid origin to *gossypinus* stock. Apparently in this region there has been more interspecific hybridization than there had been in the Henderson County and other similar populations. This is indicated by the fact that there has been an apparent fusion of the morphologic characters of the two species in southeastern Louisiana. It can be seen (fig. 3, table 1) that there is not, in these populations, the clear morphologic distinctness that was demonstrated by the Newton and Henderson County populations. There is considerable less of a difference in the average measurements

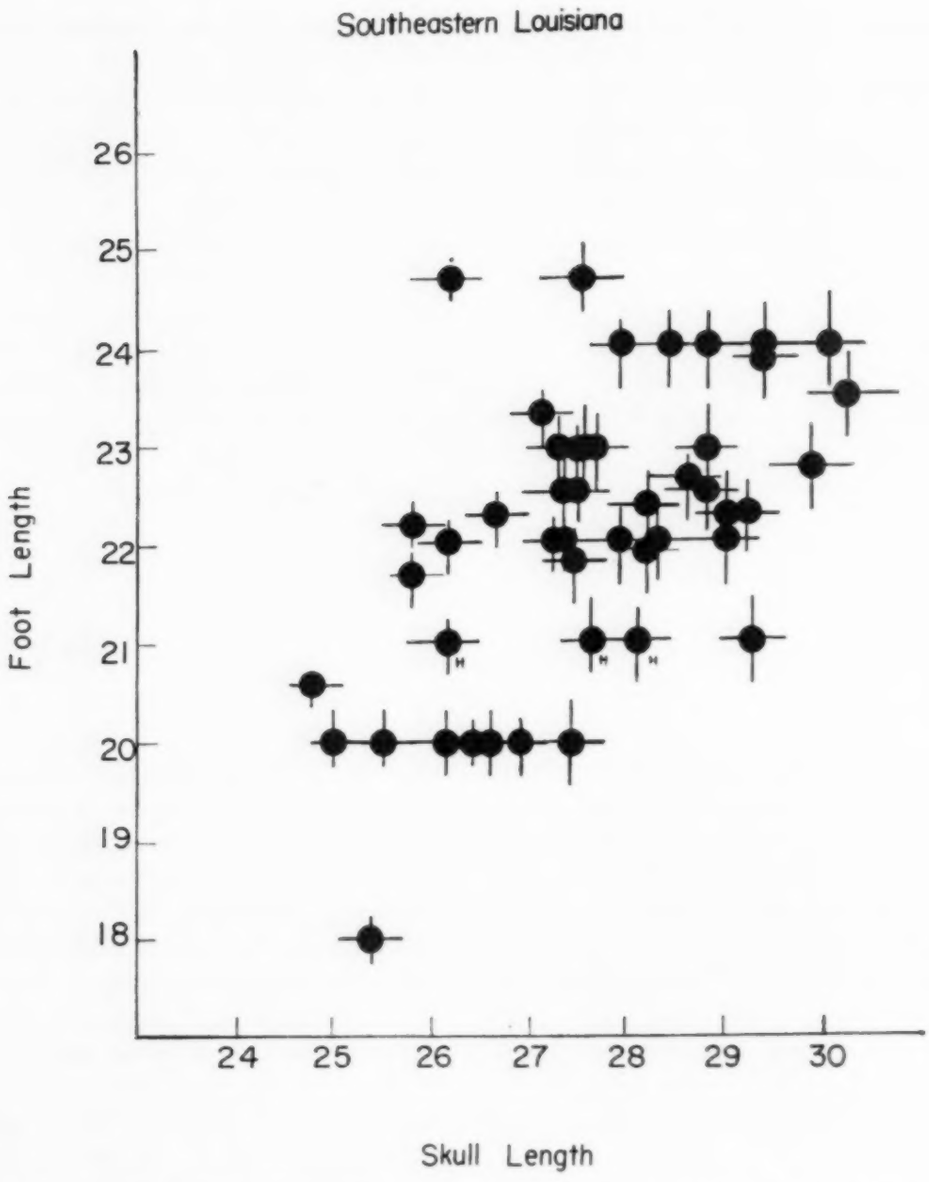


FIG. 3. The morphological relationship of a sample of *Peromyscus leucopus* and *P. gossypinus* collected in the vicinity of Baton Rouge, Louisiana. The individuals indicated by the letter H are considered natural hybrids between the two species. (For explanation of figure, see text, page 321.)

of the southeastern Louisiana species populations than in any of the other populations that were studied (table 1). This would seem to indicate that in the southeastern Louisiana populations there has been a higher rate of interspecific hybridization than has apparently taken place elsewhere. No other population samples were examined that showed a similar condition.

Slightly more than two per cent (nine individuals) of the total number of specimens examined in the course of this study were intermediate in morphological characters between the two species. These nine individuals include three (U. S. N. M., Nos. 178357, 178461, 207285—table 2) of the four specimens considered by Howell (1921) to be natural hybrids. The fourth individual (U. S. N. M., No. 207279) considered by Howell to be a hybrid has morphologic characters that are within the range of *gossypinus* characters for this region and it is doubtful that this specimen could be considered an F_1 hybrid. I would consider an ad-

ditional specimen from Alabama (U. S. N. M., No. 211505—table 2) to be a natural hybrid between *leucopus* and *gossypinus*. Howell did not consider this specimen to represent a natural hybrid, but it is intermediate in the majority of its morphologic characters. The remaining individual that is considered in the present study to be a natural hybrid between *leucopus* and *gossypinus* is a specimen (T. N. H. C., No. 2989—table 2) that was collected in Nacogdoches County, Texas.

Discussion

In view of these foregoing facts it would appear that natural hybridization does occur between *leucopus* and *gossypinus* as originally claimed by Howell (1921). It is also clear that, with one exception (southeastern Louisiana), the two species are maintaining their specific differences insofar as present evidence shows. It is only in the populations from southeastern Louisiana that there is any indication of frequent hybridization. In southeastern Louisiana this has resulted in an apparent blending of some of the morphological characters of the two species in this region. The reasons for the maintenance of species barriers (and consequent species differences) in some localities and breakdown of species barriers in other localities (resulting in interspecific hybridization and partial fusion of some of the morphologic characters) is, at present, unknown but is being investigated.

Summary

In an attempt to find out whether the sympatric species, *Peromyscus leucopus* and *P. gossypinus* hybridized in nature, 415 specimens were examined from 16 regions in Alabama, Louisiana, and Texas. Laboratory hybrids were known to be intermediate in morphologic characters between the parent species and this intermediacy was used as the criterion in the present study to distinguish suspected hybrids from the parent stocks. Nine of the 415 specimens are intermediate in morphologic characters and are believed to represent natural hybrids between *leucopus* and *gossypinus*. Three general kinds of morphologic relationships were found to exist and these relationships, in the order of their decreasing frequency, are: (1) no apparent hybridization, (2) occasional hybridization, and (3) frequent hybridization. It was only in populations from southeastern Louisiana that the species barriers are seemingly being broken down resulting in a fusion of the morphologic characters of the two species. Elsewhere it was apparent that where *leucopus* and *gossypinus* occur together they are maintaining their species identities in spite of occasional random interspecific hybridization.

Literature Cited

Anderson, Edgar A. 1949. Introgressive Hybridization. John Wiley and Sons, Inc., New York, New York.

Blair, W. Frank. 1951. Interbreeding of natural populations of vertebrates. Amer. Naturalist, Vol. LXXXV, No. 820, Jan.–Feb.

Calhoun, John B. 1941. Distribution and food habits of mammals in the vicinity of the Reelfoot Lake Biological Station. Tenn. Acad. Sci., **6**: 207–225.

Dice, Lee R. 1937. Fertility relations in the *Peromyscus lecopus* group of mice. Contr. Lab. Vert. Gen., Univ. Mich., Ann Arbor, 1937, No. 4.

Dice, Lee R. 1940. Relations between the wood-mouse and the cotton-mouse in eastern Virginia. Jour. Mamm., **21**: 14–23.

Howell, A. H. 1921. A biological survey of Alabama. U. S. Dept. Agric. Bur. Biol. Surv., North Amer. Fauna. No. 45.

Mayr, Ernst. 1942. Systematics and the Origin of Species. Columbia Univ. Press, New York, New York.

McCarley, W. H. 1954. The ecological distribution of the *Peromyscus leucopus* species group in eastern Texas. Ecology, **35** (3): 375–379.

Osgood, W. H. 1909. Revision of the mice of the American genus *Peromyscus*. U. S. Dept. Agric., Bur. Biol. Surv. North Amer. Fauna. No. 28.

PREHOMINID DENTITION AND HOMINID EVOLUTION

J. T. Robinson

Transvaal Museum, Pretoria

Received March 26, 1954

Introduction

The teeth of an animal are exceedingly important structures: to the animal, because of their use in acquiring and masticating food, self defense and their influence on the structure of the animal; to the student of animal history, because of the information they give about the animal and its relationships, and the relative ease with which they are preserved.

Since World War II there has been a phenomenal increase in the number of australopithecine fossil remains known and many of these are teeth. The new information thus gained has thrown much light on the relationship of these creatures to man and on hominid evolution in general. In this paper I wish to discuss some evolutionary trends in the australopithecine dentition as a whole and some of the effects thereof. In the first part trends in the evolution of crown size will be considered, then the effect of the dentition on skull architecture, and, finally, what conclusions may be drawn about the ecological requirements of the australopithecines with particular reference to competition and coexistence.

Nomenclature

The taxonomy of the australopithecines has been dealt with elsewhere (Robinson, 1954). It seems clear that they belong, as a group, in a separate subfamily from that including tool-making man. This was suggested, among others, by Heberer (1951) who placed the former in the subfamily Praehomininae and tool-making man in the subfamily Euhomininae. The subfamily Australopithecinae had, however, previously been erected by Gregory and Hellman (1939) as a subdivision of the Pongidae. As this subfamily contains no true pongids it may simply be transferred to the Hominidae. The latter family then comprises the Australopithecinae and the Euhomininae—a system which agrees much more closely with accepted nomenclatural principles than does that of Heberer. To avoid constant repetition of the latinized names, "australopithecines" and "prehominids" are used interchangeably for the former group and 'euhominids' for the latter.

Crown Size Trends in Hominids

The euhominid material adds greatly to our knowledge of hominid dental evolution. A glance at a complete set of upper or lower teeth of the prehominids suffices to show that the relative proportions of crown size along the tooth row is not the same as in the case of modern euhominids. The most striking difference is the relatively small size of the anterior teeth as compared to the cheek teeth. This feature has been regarded by some workers as a specialization showing that the prehominids as a group could not have been the stock from which euhominids arose. I have previously attempted to show (Robinson, 1952) that a different construction may be placed on this matter and, with recent additions to the collections, the evidence is now clearer.

In the following discussion crown sizes are compared by using the module

$$\frac{\text{Length} + \text{Breadth}}{2}.$$

This module clearly does not give an actual direct measure of the crown volume, but, as the teeth which are compared in this way are homologous, belong to closely related animals, and hence of much the same shape, the results given

are accurate enough for the purpose. This module is a commonly used method of combining the length and breadth of a crown, which are significant measurements, to give a single figure which greatly facilitates comparison. Wherever possible and unless otherwise stated the dimensions used are mean values.

The earliest known euhominids have larger teeth, on the average, and are more prognathous than in the case among modern euhominids. There has, therefore, been a reduction in the degree of projection of the face and in the size of the dentition in the course of euhominid evolution. All of the teeth have, however, not been reduced proportionately. This is indicated by the fact that the relative size of the lower molar crowns in modern euhominids is usually $M_1 > M_2 > M_3$ while in the Sangiran mandible of *Pithecanthropus* the situation is just the opposite; $M_1 < M_2 < M_3$.

The modules of the mandibular dental elements of some hominids are plotted in fig. 1. Those for the known teeth of *Telanthropus* are also plotted and these alone are not modules of mean values. The graph for the maxillary dentition is so similar that it is not given here.

From this diagram it is clear that differential reduction of the molars has occurred: M_1 has been affected least and M_3 most. In the prehominids the molar crown size formula is $M_1 < M_2 < M_3$. In only one individual (SK 23), where all three molars are in situ, is there any indication that M_3 is approaching the size of M_2. In *Telanthropus* only one jaw is known with all three molars in situ and in that the formula is $M_1 < M_2 > M_3$ but in the second mandible it is clear that M_3 must have been much reduced (see Robinson, 1953b), and, if that was the case, the formula would be the same for both mandibles. *Telanthropus* is thus more advanced than the prehominids with respect to the reduction of the crown size of the mandibular molars. It would be extremely interesting to know what the condition was in *Pithecanthropus,* but unfortunately only the single mandible from Sangiran is known with all three molars in situ. This has the formula $M_1 < M_2 < M_3$ (Weidenreich, 1945) and therefore agrees

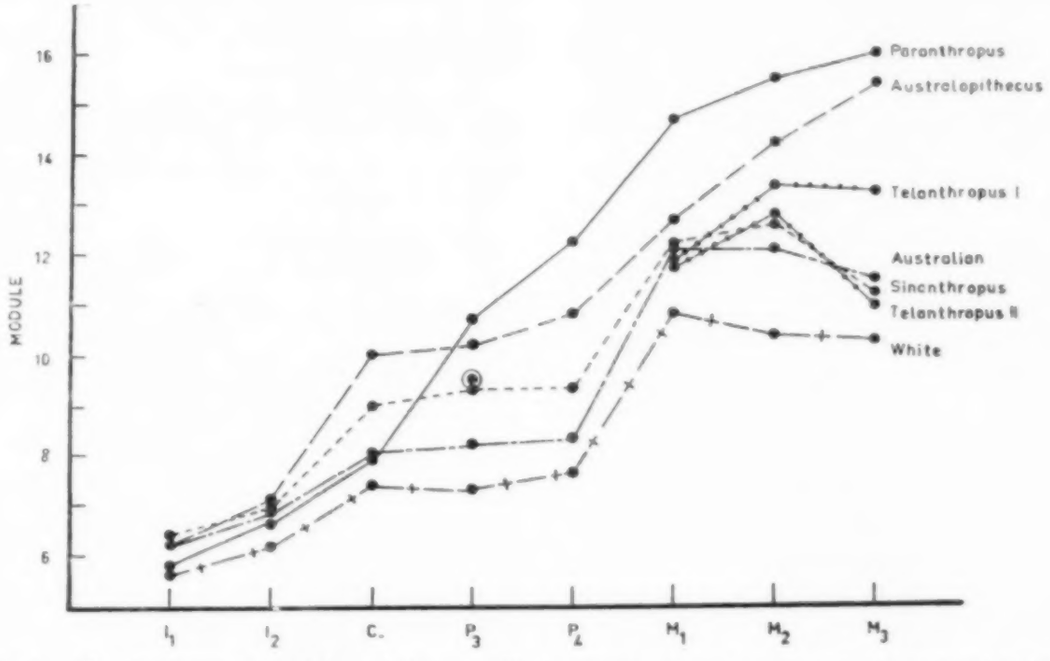


FIG. 1. Graph showing modules of the mandibular teeth of some prehominids and euhominids. All values are averages except in the case of *Telanthropus*. The encircled, isolated point represents the module of P_3 of *Telanthropus* I.

with the condition in the prehominids. But the molars of the only upper jaw known are in the following size order: $M^1 < M^2 > M^3$ with M^3 considerably reduced. This agrees well with the situation in the *Telanthropus* lower dentition. Although the maxilla normally leads the mandible in the reduction process, it is reasonable to assume that M_3 must also have been reduced to some extent in some members of a population including such individuals as the above in which M^3 is so much reduced as to be smaller than M^1.

Sinanthropus (Weidenreich, 1937) has M_3 appreciably reduced, on the average, compared to M_2. As in the maxillary dentition of the *Pithecanthropus* palate from Sangiran, M_3 is actually smaller than M_1 as a rule. Here also, for upper and lower dentitions the size sequence is $M_1 < M_2 > M_3$. This sequence also occurs in Neanderthal man. The next stage in the reduction of the molars is that in which M2 is reduced to the same size as M1 or even further. The size sequence then is either M1 = M2 > M3 or M1 > M2 > M3. In the Australian Aboriginal (Campbell, 1925) the lower molars are in the former size order, while the maxillary molars are in the latter sequence. In modern American Whites (Black, 1902) both upper and lower molars are arranged in the sequence M1 > M2 > M3. The South African Bantu (Shaw, 1931) are a little unusual in that the average sizes of the three molars are almost exactly the same. In Neanderthal man there are no average figures based on a fair sized population but the size order of the molars seems to vary from M1 < M2 > M3 to M1 > M2 > M3.

The evolution of molar size can therefore be traced quite clearly from the prehominid stage to that of modern euhominids. Much of this evolution has gone on independently in a number of different lines. Hence the fact that the size sequence is not identical in all the living ethnic groups.

The differential reduction of the third and second molars was probably caused initially by space shortage. The first permanent tooth to come into functional position is usually the first molar. The remaining permanent teeth must, therefore, fit into the remaining space on either side of it. M3 is normally the last tooth to erupt and it is, therefore, conceivable that space shortage would affect it more than the other teeth. This would particularly be the case in the reduction of the jaws from the massive prehominid type to the smaller euhominid type. It has been pointed out from time to time that failure to erupt—or impaction—of M3 is not always a result of space shortage in modern man. This does not invalidate the suggestion that lack of space was the operative factor in the early stages of face reduction. The continued reduction of the third molar may be an example of the phenomenon recently demonstrated by Waddington (1953a and b), the genetic assimilation of an originally environmental effect, the character 'crossveinless' in *Drosophila melanogaster*. What was originally a reduction brought about by space shortage may now be genetically assimilated and influenced by selection, which is related not only to space shortage in the jaw but also to other factors.

The evolution of crown size in the teeth anterior to the molars is not nearly so clear cut but nevertheless is of considerable interest.

Reference to figure 1 will show that with the exception of *Paranthropus* the curves are very similar anterior to M_1, if one allows for the relatively small amount of reduction of M_1. The incisors of all the forms dealt with are very similar in size. This suggests that reduction of the canines and premolars has been of comparable extent without producing marked differential changes such as those posterior to M_1. There is comparatively great variability in the size of the upper lateral incisor and this tooth also shows considerable individual variability in modern euhominids, in some

cases being congenitally absent. It has been assumed that this is a result of rapid reduction of this tooth, but the fact that the Sterkfontein form has lateral upper incisors as small as the average for American Whites indicates that this tooth has probably been small for a very long time in hominid history. Perhaps it never has been a large tooth.

The curve for *Paranthropus* does not follow the others nearly so well, and in both the upper and lower dentitions the curves for the latter cross that of *Australopithecus* between the positions for the canine and first premolar. The reason for this reversal will be inquired into in a later section of this paper.

If it is assumed that the large size of the cheek teeth of *Paranthropus* represents an earlier prehominid condition, then it is possible to interpret the condition in the known prehominids as a result of a reduction process that started at the front of the jaw and passed backward. According to such a supposition, the process has gone further in *Paranthropus* because the incisors and canines have been affected as well as the first premolar to a certain extent. In *Australopithecus* the canines and first premolars have not been affected. As previously mentioned, the incisors have probably never been large teeth and the reduction which they have suffered is probably very slight. It is possible, on the other hand, that the *Paranthropus* curve is of a different nature because the post-canine teeth were enlarging, not reducing in size. This does not seem likely to me, because the general trend in the early stages of hominid evolution is generally toward reduction of the face and there are signs of this in *Paranthropus* in the uniformly shortened face. While it is not impossible that the tendency was reversed in this one phyletic line, strong evidence of it would be necessary before accepting such a change. It is more probable therefore that the *Paranthropus* curve is unusual only because the anterior part of the tooth row was reduced very rapidly or because some factor retarded the reduction further back. This conclusion is supported by the fact that the small-crowned canines are generally very robust-rooted, suggesting that the reduction of the canines was not yet complete. *Australopithecus* has robust canines, crown and root; *Paranthropus* has robust-rooted, small-crowned canines; *Telanthropus* probably had canine crowns of the same size as those of *Paranthropus*, but the root sockets are small.

In view of these facts it seems likely that reduction occurred in two phases: one process starting at the rear end of the tooth row and gradually passing forward, and the other starting from the front end and passing backward toward M1. The dominating position of M1 is probably partly due to the fact that it is normally the first of the permanent teeth to come into functional position.

Instead, therefore, of a series of static types of relative size formulae for the different dentitions, we see a dynamic process of change going on which converted a prehominid type of dentition into a modern euhominid one. *Paranthropus* and *Australopithecus* are not members of one phyletic line (Robinson, 1954) nor does either appear to fall on a line which actually gave rise to euhominids. They nevertheless probably give a good idea of stages through which the actual euhominid ancestor did pass while in the prehominid phase.

Dentition and the Form of the Skull

The graphs showing comparative tooth sizes along the tooth row are interesting in that they give rise to another line of thought besides the one dealt with above. What is the reason for the prehominid with the smallest incisors and canines having the largest cheek teeth? A possible explanation is suggested below in conjunction with discussion of the resulting changes in the architecture of the skull.

It is clear that the teeth of the pre-

hominids were put to heavy use, especially the molars of *Paranthropus*. The latter are massive, with very thick enamel (as much as 3 mm. on the occlusal surface), and yet, by the time M3 erupts, M1 has already been worn quite flat, with the dentine exposed in places. In older individuals, where the occlusal surface of M3 is moderately flattened, M1 usually no longer has enamel on the occlusal surface. When M3 is strongly worn, the crown of M1 is almost entirely gone. The occlusal surface enamel of a tooth in full use has numerous well marked scratches, which run at right angles to the length of the tooth row, i.e. in a bucco-lingual direction. Both upper and lower jaws are massive, particularly at the level of the molars. *Australopithecus* also has these characters, but to a less marked degree except for the relative rate of wear of the teeth, which is much the same in both groups. A feature common in the Swartkrans dental material is chipping of enamel from the edge of the occlusal surface. That this chipping occurred in life is clearly shown by the fact that most of the roughened areas left after such flaking are smoothed by subsequent use of the tooth. Chipping is not confined to the anterior teeth.

All these features suggest heavy use of the teeth of the prehominids in general, and particularly in *Paranthropus*. The relatively great disparity in size between the front and the cheek teeth, the rapid flattening of the premolars and molars and the considerably thickened bone around the molar roots indicate that crushing and grinding was the main function involved. The most suitable sort of diet for such a primate dentition would probably consist predominantly of vegetable materials, including shoots and leaves, berries, tough wild fruits, roots and bulbs. The latter ingredients may have resulted in grit particles being chewed, causing chipping of the enamel. The South African Chacma baboon eats roots and bulbs among other things and enamel chipping of just the same sort as that found in *Paranthropus* occurs on the teeth of this form. The relatively small anterior teeth—particularly canines—would be consistent with such a diet and would also suggest that *Paranthropus* was not an aggressive, predaceous creature, and had means of defense (and offense if required) other than dental ones. These were probably in the form of any sticks, bones or stones conveniently to hand, coupled with a certain amount of intelligence and cunning.

Australopithecus, with less disparity in size between anterior and posterior elements of the dentition, with appreciably larger canines and smaller premolars and molars than *Paranthropus*, probably had a more nearly omnivorous diet, which may have included a fair proportion of flesh as indicated by evidence brought forward by Dart (1949).

These differences in diet may well account for the differences in the pattern of dental reduction processes in the two prehominid lines. The heavy use to which the molars, especially, were put in *Paranthropus* may have resulted in their reduction being retarded as compared to the less important anterior teeth.

As Benninghoff (1925) and others have shown, the face skeleton is highly organized with regard to the forces of mastication. It is interesting to compare the skulls of *Paranthropus* and *Australopithecus* in the light of this work.

Both are stressed forms with the result that the nasal region has much the same shape and structure; the nasal region does not protrude and the margin of the pyriform aperture is thick. If Washburn's (1953) reading of the evidence is correct, as seems probable, then one may note in passing that the flattened and rather pongid nasal region of the prehominids is in no way a bar to their being euhominid ancestors—as has been suggested. The flattened shape, in this view, results from this region being stressed. With relaxation of the forces affecting this region, as a result of reduced dental size in descendants, the

nasal region would be more protuberant and without the strong buttressing on either side of the pyriform aperture. As one might expect from the larger-canined form, *Australopithecus* usually has relatively more pronounced buttresses on either side of the pyriform aperture, but this is not an absolute distinction.

Farther back along the tooth row, the results of the much greater masticatory stresses in *Paranthropus* become more obvious. The alveolar region, which contains the molars, is much thickened and the malar-zygomatic buttress is very robust. The zygomatic process of the maxilla and the zygomatic bone are much thickened, compared to the condition in *Australopithecus*. The top end of this buttress, the supraorbital torus, is also relatively robust in *Paranthropus*.

The wide and very flat bony face of *Paranthropus* is largely a result of the decreased size of the anterior teeth and the naso-frontal buttress, and the greatly increased robustness of the malar-zygomatic buttress. However, the matter does not stop there. The robust mandible of *Paranthropus* and the strength required for the great masticatory activity have resulted in a well developed temporal

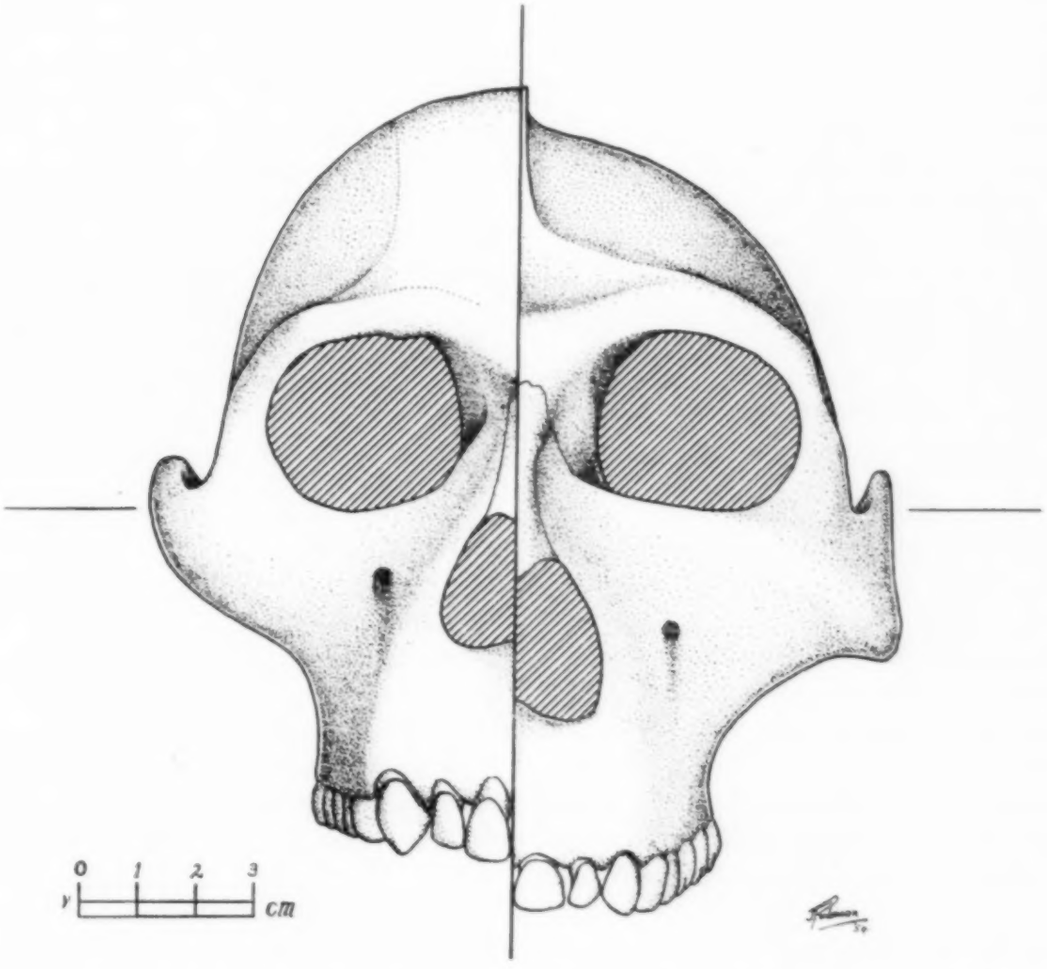


FIG. 2. The left half of this drawing depicts half of the face of *Australopithecus* from Sterkfontein (Sts 5) and the right half that of *Paranthropus* (SK 48) from Swartkrans. The latter had to be restored in places, but this was done from other specimens from the same site. The dentition of Sts 5 is missing, but it has been restored here from Sts 52 which has the dentition complete and only very slightly worn. The incisors of SK 48 are missing and are here restored from SK 55. Both halves are oriented on the Frankfort plane and the vertical register is determined by the latter plane. The *Australopithecus* face is distinctly more prognathous than the other. As far as can be determined both skulls belonged to female individuals.

muscle. One may note here that, although the masseter muscle was well developed, it may have been relatively poorly developed compared to the other muscles of this region in *Paranthropus*. The angle of the mandible is turned inward to a small extent and has strong rugosities on the medial face for the attachment of the medial pterygoid, whereas the markings on the outer face of this region, for the attachment of the masseter, are poorly developed. The temporal muscle may therefore have been relatively more important in this form than in euhominids, but the evidence is not sufficient for this to be more than a tentative conclusion.

The temporal muscle is so well developed in *Paranthropus* that it frequently reaches the sagittal plane. Perhaps this is the usual adult condition, for it is present in the only three adult specimens known in which the relevant region is preserved. Under such conditions, a bony sagittal crest develops. Washburn (1947) has shown that the presence, size, and position of nuchal and mastoid crests in the rat are determined entirely by mechanical stress due to muscle function. This work confirms and extends conclusions drawn by earlier workers using other mammalian material. The presence of a bony sagittal crest in *Paranthropus* does not, therefore, suggest that there is some close genetic relationship between this form and the pongids, among which crests are common. It merely indicates that the same combination of robust teeth and temporal muscles with a relatively small braincase is to be found in both groups. The sagittal crest is not something intrinsically determined as such.

In *Australopithecus* with its less powerful masticatory apparatus, the temporal lines are, on the available evidence, usually well separated. Of five specimens showing this region only one fragment of skull from Makapan, consisting of the occipital region, clearly had the temporal lines meeting in the region of the vertex.

The condition in the occipital region of the skull is interesting in cases where a sagittal crest is present. The temporal muscles do not meet the nuchal musculature nor do the temporal muscles meet each other in the midline posteriorly. This is very clearly demonstrated in the Makapan occipital fragment and less clearly in SK. 48, from Swartkrans. There is no continuous nuchal crest nor does the sagittal crest pass right back to the occiput. It stops short of the position which would have been occupied by a nuchal crest had there been one. This is not in agreement with the views of Zuckerman (1952), who feels that, because in primates and mammalia in general nuchal crests are almost invariably associated with sagittal crests, this should also be the case in the prehominids. He says, "But unless *Paranthropus* provides a single exception to what seems to be a general feature of the architectural dynamics of the Primate skull, our observations about the coexistence of sagittal and nuchal crests in Primates seem to indicate clearly that *Paranthropus crassidens* had a strong nuchal musculature of the kind seen in extant great apes, and that it would have had nuchal crests."

As we have seen, these crests and their position are resultants of mechanical factors which are themselves part of a pattern involving the whole head, at least. In the prehominids, the brain case is relatively long compared to that of pongids, such as the gorilla, and the occiput is much more nearly horizontal in position. The large temporal muscles can meet in the midline in the region of the vertex, for the skull is relatively low and narrow anteriorly, but they do not reach the occiput, which is wide and does not extend so far up the skull. The more nearly horizontal occiput is associated with the bipedal posture of the prehominids, of which there is now considerable evidence. The predominantly vegetable diet of a large animal has resulted in heavy temporal musculature. As the braincase is relatively small anteriorly,

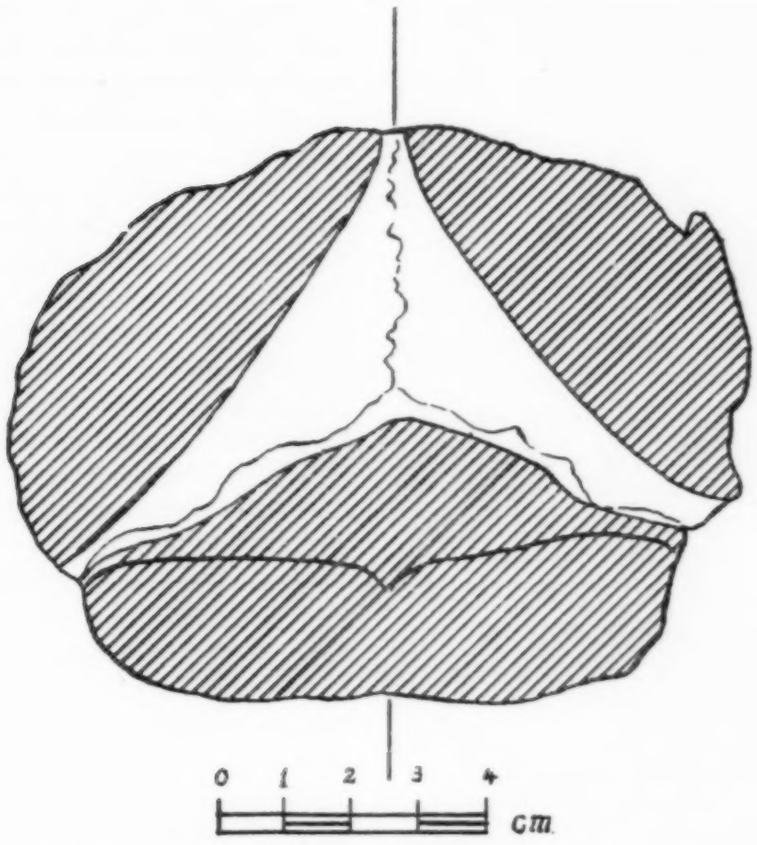


FIG. 3. Semi-diagrammatic drawing (modified after Dart) of the first occipital fragment of *Australopithecus* from Makapan. The hatched areas are those covered by the temporal and nuchal musculature. A sagittal crest must have been present near the vertex but is not present posteriorly, nor is there a nuchal crest.

these combined result in an incomplete sagittal crest but no nuchal crest. As this particular combination of features is not found in other primates, or mammals in general, it is not surprising that prehominids should provide an exception to the general rule about the association of nuchal and sagittal crests. Modern euhominids do not have either crest. Not only has the braincase expanded considerably but also the dentition has been reduced in size along with the forces of mastication. Consequently, the conditions for producing either crest do not arise. This, however, is no reason whatever for supposing that those conditions did not arise at some earlier stage of euhominid evolution.

Much of the difference in general skull form between the *Paranthropus* and the *Australopithecus* lines is, therefore, due to the differences in nature and amount of use to which the dental battery is put. These in turn affect the evolution of the teeth by modifying the general pattern common to the euhominids as a whole. The retardation of the reduction of the post-canine teeth in *Paranthropus* as compared to *Australopithecus* is probably a result of the relatively greater amount of work required of these teeth in the former case. If an australopithecine was ancestral to the euhominids, as is clearly suggested by the nature of *Telanthropus,* then a continuation of the dental reduction observed would have resulted in a euhominid type of dentition, with consequent effect upon the architecture of the face in particular and of the skull in general. The expanding brain would have helped further to transform the skull into one of euhominid type.

Ecological Requirements and Coexistence

In a recent brief review of a paper of mine, Mayr (1953), in "Comments on evolutionary literature," remarks that my suggestion that euhominids arose from prehominids, but that some groups of the latter survived for some time subsequent to the origin of the former, raises a serious problem of competition, which I did not discuss. I shall attempt to rectify this omission here as it has some bearing on points raised in the preceding section.

This problem really has two parts; coexistence and competition between (a) prehominids belonging to different phyletic lines, and (b) prehominids and early euhominids.

As far as our present evidence goes there is no indication that *Paranthropus* and *Australopithecus* simultaneously occupied the same territory. The time relationship of Taungs and Makapan relative to the other sites is not known with any degree of certainty at present, though work is in progress which will probably throw light on this matter. The relationship of Sterkfontein (*Australopithecus*) and Swartkrans (*Paranthropus*) is more certain, the former being a little older than the latter. The Kromdraai faunal site is later again than Swartkrans, and probably the time gap is greater between the latter two than between Sterkfontein and Swartkrans. However, the Kromdraai prehominid remains came from a different breccia mass than did the faunal remains and at present we do not know the age relation of these two deposits which are separated by only 100 feet. Fortunately the two sites of which the relative ages are known are the two which have yielded almost all of the known prehominid specimens. These two sites are separated geographically by just over three quarters of a mile. There is no barrier between the two sites and the type of country is the same at both. It is therefore reasonable to suppose that had *Australopithecus* still occupied the Sterkfontein region by Swartkrans times, remains of the latter would have been found in the Swartkrans site. The reverse argument also holds and so one can be reasonably confident that *Paranthropus* was not living in the Sterkfontein region at the time the Sterkfontein type site deposit was accumulating. On available evidence there is consequently no problem regarding competition between these two forms. It is possible that *Paranthropus* displaced *Australopithecus* from this region. This does not seem very likely, if the conclusions regarding diet are correct, because there would be comparatively little conflict over food and there is no reason to suppose that numbers were so high as to cause conflict over space.

At Swartkrans, however, there is clear evidence of two different hominids synchronously present in the Sterkfontein area, *Paranthropus* and *Telanthropus*. I have elsewhere (1953) shown that it is highly probable that *Telanthropus* had actually or very nearly achieved euhominid status, and probably ought not to be regarded as a prehominid. There is no indication from the teeth and jaws that the diet of *Telanthropus* was any different from that of other early euhominids, and the relatively enormous molars of *Paranthropus* are certainly not present. There is circumstantial evidence that it was larger-brained than *Paranthropus*. Under these circumstances there is no reason to suppose that the ecological requirements of these two forms would so nearly coincide that mutual occupation of similar or overlapping territory could not continue for more than a very short time.

Less than a dozen miles from the Sterkfontein site, in a relatively remote area, spotted and brown hyenas today occupy the same territory. It is well known that they do so elsewhere, and that they are both scavengers, although the brown hyena is predaceous to a small extent whereas the other is normally not. But in this particular area, which is of small

extent and entirely surrounded by settled farms and therefore relatively civilized, the competition for available food is higher than it would be under normal conditions.

Similarly the toads *Bufo regularis* and *B. carens* may be caught in the same gully or under the same street lamp over a considerable area of South Africa. Their ecological requirements are very similar but they are nevertheless sympatric at present. Numerous other examples of the same sort may be given where the difference in ecological requirements appears to be of a smaller order than that between *Telanthropus* and *Paranthropus*. It may well be that in the course of time one or other of such pairs of sympatric species would be displaced, but in the case of hyenas the present situation seems to have started very early in the Pleistocene in this area. The rise of euhominids may quite easily have been the cause of the extinction of the prehominids, but the competition could not have been so sharp that the latter were exterminated almost immediately.

Sangiran provides an instance of an analogous situation to that of Swartkrans. There a species of *Paranthropus*, very similar, on the scanty evidence available, to the one at Swartkrans, coexisted with a species of *Pithecanthropus*. In fact, according to von Koenigswald (1950; Weidenreich, 1945), *two* species of *Pithecanthropus* occur in the Sangiran deposit, although the evidence for this is not convincing. These two almost identical instances, one in Java and the other in South Africa, seem clear enough indication that at least the *Paranthropus* type of prehominid could coexist with early euhominids. On available evidence the Sangiran forms were a little later in time than those at Swartkrans.

It seems legitimate, to me, to conclude that competition was not a factor of great importance. Competition there doubtless was, but not of the sort or intensity that has been so obvious a feature of the history of racial groups of euhominids, where competition has so frequently been for the same things, since the competing groups are members of the same species.

Summary

Indications are present in the dentition of prehominids that the dentition as a whole was being reduced. The reduction processes fit in well with what is known of reduction in euhominid dentitions, and the latter reduction appears simply to be a continuation of that started in the pre hominid group. The reduction process proceeds in different directions on either side of the first permanent molar, being from back to front in the molar row and front to back in the teeth anterior to M1. This has resulted in reduction of the size of all the elements of the dentition, but all have not been reduced to the same degree.

The forces of mastication influence the architecture of the skull as a whole, but more especially that of the face. The diet of *Paranthropus* appears to have been primarily vegetarian, while that of *Australopithecus* seems to have been omnivorous and to have included a fair proportion of flesh. The resulting differences in strength and nature of the masticatory forces has affected the shape and structure of the face and braincase.

There is no evidence that prehominids and euhominids could not synchronously occupy the same territory. On the contrary, the situation at Swartkrans (South Africa) and Sangiran (Java) indicates clearly that this did occur.

Acknowledgments

Some of the information incorporated in this paper was obtained as a consequence of financial assistance from the Nuffield Foundation and the Wenner-Gren Foundation for Anthropological Research and I should like to seize this opportunity of recording my gratefulness for their assistance. My thanks are also due to my colleagues C. K. Brain, L.

Freedman and A. J. Meester for discussions involving some of the points here included.

Literature Cited

Benninghoff, A. 1925. Spaltlinien am knochen, eine methode zur Ermittlung der Architektur platter knochen. Verhandl. d. anat. Gesellsch., **34**: 189.

Black, G. V. 1902. Descriptive Anatomy of the Human Teeth. 4th edit. Philadelphia: S. S. White.

Campbell, T. D. 1925. Dentition and Palate of the Australian Aboriginal. Adelaide.

Dart, R. A. 1949. The predatory implemental technique of *Australopithecus*. Amer. J. Phys. Anthrop., **7**: 1–38.

Gregory, W. K., and M. Hellman. 1939. The dentition of the extinct South African man-ape *Australopithecus* (*Plesianthropus*) *transvaalensis* Broom. Ann. Transvaal Mus., **29**: 339–373.

Heberer, G. 1951. Der phylogenetische Ort des Menshen. Studium Generale, **4**: 1–14.

Mayr, E. 1953. Comments on evolutionary literature. (Man's ancestors, p. 281.) Evolution, **7**: 273–281.

Robinson, J. T. 1952. Some hominid features of the ape-man dentition. Offic. J. Dent. Assn. S. Afr., **7**: 102–113.

——. 1953a. *Meganthropus*, australopithecines and hominids. Amer. J. Phys. Anthrop., **11**: 1–38.

——. 1953b. *Telanthropus* and its phylogenetic significance. Amer. J. Phys. Anthrop., **11**: 445–501.

——. 1954. The genera and species of the Australopithecinae. Amer. J. Phys. Anthrop., **12**: 181–200.

Shaw, J. C. Middleton. 1931. The Teeth, the Bony Palate and the Mandible in Bantu Races of South Africa. London.

Visser, J. B. 1946. De Wortelvariaties van de postcanine onderelementen van het menschelijk gebit. Tijdsschrift voor Tandheelkunde, **53**: no. 11, and 1947, **54**: no. 1.

von Koenigswald, G. H. R. 1950. Fossil hominids from the lower Pleistocene of Java. Internat. Geol. Congr. "Report of the Eighteenth Session, Great Britain, 1948," Part IX.

Waddington, C. H. 1953a. Genetic assimilation of an acquired character. Evolution, **7**: 118–126.

——. 1953b. The evolution of adaptations. Endeavour, **12**: 134–139.

Washburn, S. L. 1947. The relation of the temporal muscle to the form of the skull. The Anatomical Record, **99**: 239–248.

——. 1953. The strategy of physical anthropology. Pp. 714–727. (M. Kroeber, ed.: Anthropology Today, University of Chicago Press.)

Weidenreich, F. 1937. The dentition of *Sinanthropus pekinensis:* a comparative odontography of the hominids. Pal. Sinica, n.s. D, no. 1–180 + atlas.

——. 1945. Giant early man from Java and South China. Anthropol. papers Amer. Mus. Nat. Hist., **40**: 1–134.

Zuckerman, S. 1952. Discussion of "The australopithecines and their evolutionary significance" by J. T. Robinson. Proc. Linn. Soc. London, **163**: 200–203.

INTERACTION OF THE ADAPTIVE VALUES IN POLYMORPHIC EXPERIMENTAL POPULATIONS OF *DROSOPHILA PSEUDOOBSCURA*

HOWARD LEVENE,[1] OLGA PAVLOVSKY,[2] AND THEODOSIUS DOBZHANSKY[2]

Departments of Mathematical Statistics and Zoology, Columbia University, New York City

Received April 14, 1954

INTRODUCTION

Genetic diversification is an evolutionary mechanism which enables Mendelian populations to master a wide variety of environments in the territories which they inhabit. In many species of Drosophila, some of the genetic diversification takes the form of chromosomal polymorphism. Thus, in *Drosophila pseudoobscura* several (up to seven) different gene arrangements occur in the third chromosomes in many natural populations. The chromosomal polymorphism can be studied not only in natural but also in artificial laboratory populations (Wright and Dobzhansky, 1946; Dobzhansky, 1949). Such studies have shown that the fitness of the structural heterozygotes which carry two third chromosomes with different gene arrangements derived from the same population is, not invariably but usually, superior to that of the corresponding structural homozygotes. The polymorphism is, therefore, balanced, and the gene arrangements are maintained in the populations with frequencies which are determined, for a given environment, by the relative adaptive values of the different karyotypes (Dobzhansky, 1948, 1949; Dobzhansky and Levene, 1948).

The great interest of the chromosomal polymorphism in Drosophila is that it makes the processes of natural selection and evolutionary adaptation amenable to experimental study. The work in this field has disclosed that the fitness of the different karyotypes is extremely sensitive to environmental conditions. Furthermore, the karyotypes which occur in a given natural population are mutually adjusted by natural selection to confer a high average fitness on the Mendelian population as a whole (Dobzhansky and Levene, 1951; Dobzhansky and Pavlovsky, 1953).

It remains, however, largely unknown whether the adaptive value of a karyotype may depend upon the genetic composition of the population itself. In other words, it has not been determined whether the fitness of a karyotype is independent of what other karyotypes are present in the same population, or whether the karyotypes present in an environment interact in any way. With few exceptions (Wright and Dobzhansky, 1946), the experimental laboratory populations of *Drosophila pseudoobscura* have been made to include only two gene arrangements at a time. The reasons for this are technical. With two gene arrangements the population contains three karyotypes: two inversion homozygotes and a heterozygote. With three gene arrangements the number of karyotypes rises to six: three homozygotes and three heterozygotes. Increasing diversity of karyotypes makes the diagnosis under the microscope of the chromosomal configurations difficult, and the estimation of the adaptive values from the data laborious. Yet, many natural populations contain, as stated above, several gene arrangements, and the experiments on the artificial populations containing two gene arrangements at a

[1] Research under contract with Office of Naval Research.

[2] The work reported in this article has been carried out under Contract No. AT-(30-1)-1151, U. S. Atomic Energy Commission.

time have yielded some inconsistent results. The most obvious inconsistency arose in experiments involving chromosomes derived from the population of Piñon Flats, on Mount San Jacinto, in California (Dobzhansky, 1948). The experiments on population cages containing chromosomes with Standard (ST) and with Arrowhead (AR) gene arrangements gave results from which the following adaptive values of the three karyotypes were estimated:

ST/ST	ST/AR	AR/AR
0.8	1.0	0.5

The experiments with Standard and Chiricahua (CH) chromosomes gave the adaptive values as follows:

ST/ST	ST/CH	CH/CH
0.8	1.0	0.4

This would lead one to expect that the AR/AR homozygotes should have an only slightly higher fitness than the CH/CH homozygotes. Population cages in which the AR chromosomes were competing against CH gave, however, the following adaptive values:

AR/AR	AR/CH	CH/CH
0.86	1.0	0.48

Although all these estimates are subject to considerable experimental errors, the observed inconsistency appears large enough to warrant a suspicion that the adaptive value of a karyotype may be modified by the presence of individuals with other karyotypes (or genotypes) in the same environment. Experimental populations in which the three gene arrangements (ST, AR, and CH) were present were accordingly set up and studied.

Material and Methods

The strains of flies which were used in older experiments (Dobzhansky 1949 and earlier) unfortunately no longer exist. We have employed strains isolated more recently by Dr. Donald Mitchell from flies collected at Piñon Flats and kindly placed by him at our disposal (these strains were also used by Dobzhansky and Pavlovsky, 1953). Twelve strains homozygous for each gene arrangement were introduced in each experimental population. The parental flies with which the experimental populations were started were, however, F_1 hybrids between the strains with different gene arrangements. These hybrids (ST/CH and AR/CH) were raised in ordinary culture bottles, counted, and placed into the population cages in desired proportions. Two replicate experimental populations (referred to below as A and B) were run simultaneously. The precaution of using hybrid flies as parents of the experimental population is important, because the structurally homozygous strains vary widely in viability. Replicate populations are desirable not only in order to reduce somewhat the experimental errors, but also because in populations in which the chromosomes are derived from progenitors collected in different localities the results of the selection processes may vary widely from experiment to experiment (Dobzhansky and Levene, 1951; Dobzhansky and Pavlovsky, 1953).

The experimental populations were kept in an incubator at 25°C, and fed on a culture medium with baker's yeast. The techniques of sampling and of examination of the chromosomes were described previously (Dobzhansky and Pavlovsky, 1953 and earlier) and need not be repeated here. Suffice it to say that every sample consisted of 150 larvae (300 chromosomes), taken in six subsamples, on as many successive days, with 50 chromosomes per subsample. The third day of sampling was considered the date of the whole sample.

The Data

The frequencies of the ST, AR, and CH chromosomes found in each of the nine samples taken in the two replicate

populations are shown in table 1. The samples were taken at approximately 35-day intervals, except that no sample was taken between the 245th and the 315th day. The average length of a generation in the population cages at 25°C may be taken as 25 days. The experiment was carried for exactly a year, from November 15, 1952, to November 15, 1953, or for about 14.6 generations. In both replicate populations the frequencies of the gene arrangements changed rapidly at first, then more slowly, and apparently not at all after approximately the 10th generation. As shown below, this may, however, mean only that the changes at that time were so slow that they were masked by the sampling errors. The two populations remained similar to each other throughout the experiment; a combined chi-square for all the observations reported in table 1 is 25.50, which for 18 degrees of freedom corresponds to a probability of slightly more than 0.10.

TABLE 1. *Observed frequencies, in per cent, of the Standard, Arrowhead, and Chiricahua chromosomes in the two populations, A and B*

Age in days	Standard		Arrowhead		Chiricahua	
	A	B	A	B	A	B
0	25.0	25.0	25.0	25.0	50.0	50.0
32	34.3	37.0	19.3	18.7	46.3	44.3
70	47.0	46.7	21.0	23.7	32.0	29.7
105	58.7	61.3	22.0	19.7	19.3	19.0
140	65.7	59.3	20.3	21.7	14.0	19.0
125	69.7	71.7	15.0	12.0	15.3	16.3
210	70.7	67.7	23.0	20.0	6.3	12.3
245	80.3	79.0	16.7	13.7	3.0	7.3
315	80.7	74.0	15.0	18.3	4.3	7.7
365	80.0	81.7	16.7	12.7	4.3	5.7

ESTIMATION OF THE ADAPTIVE VALUES

The following notation will be used: ST is denoted as 1, AR as 2, and CH as 3. The chromosome frequencies at any given time t will be p_{1t}, p_{2t}, and p_{3t} respectively. Let

$$\Delta^*_{1t_1} = p_{1t_2} - p_{1t_1}$$

be the observed change in frequency of ST from time t_1 to time t_2. The *adjusted rate of change per generation* will then be

$$\Delta_{1t_1} = \left(\frac{t_2 - t_1}{g}\right) \Delta^*_{1t_1}$$

where g is the length of a generation. We define Δ_{2t} and Δ_{3t_1} similarly. We will always take g = 25 days and give t in days from the start of the experiment. Now Δ_{1t} differs from $\bar{\Delta}_{1t}$, the true change in one generation from time t, for two reasons, first because of sampling error, and second because the change in gene frequencies is not linear. The longer the interval between samples the more serious the latter error becomes.

The adaptive values of the six karyotypes will be denoted by W_{11}, W_{22}, W_{33}, W_{12}, W_{13}, W_{23}, and will always be written in that order. Since the course of selection does not depend on the absolute values of the W's, but only on their relative values, they are only defined up to a constant factor. For simplicity we will always take $W_{12} = 1$.

The first method tried for estimating the adaptive values was the method of unweighted least squares applied to the differences between successive samples, as used by Wright and Dobzhansky (1946). Some modifications were made to simplify the computations, but they do not affect the final results. Wright and Dobzhansky (1946) on page 150 give six normal equations to be solved for the adaptive values W. Since there are only five independent W's, there are only five independent equations, and one may be eliminated. Wright suggests solving these equations by iteration, at each stage considering the x's and y's defined below as constants. Since iteration is being used, it is not necessary to solve this set of five simultaneous linear equations exactly, and the laborious process of solution can be replaced by the iterative method of Gauss, solving each equation to give one of the W's in terms of the others. The

net result, setting $W_{12} = 1$ and omitting the corresponding equation, is

$$W_{13}=[(U_{13\cdot1}+U_{13\cdot3}-U_{13\cdot12})-U_{13\cdot11}W_{11}-U_{13\cdot33}W_{33}-U_{13\cdot23}W_{23}]/2U_{13\cdot13},$$
$$W_{23}=[(U_{23\cdot2}+U_{23\cdot3}-U_{23\cdot12})-U_{23\cdot22}W_{22}-U_{23\cdot33}W_{33}-U_{23\cdot13}W_{13}]/2U_{23\cdot23},$$
$$W_{11}=[(U_{11\cdot1}-U_{11\cdot12})-U_{11\cdot13}W_{13}]/U_{11\cdot11},$$
$$W_{22}=[(U_{22\cdot2}-U_{22\cdot12})-U_{22\cdot23}W_{23}]/U_{22\cdot22},$$
$$(1)\quad W_{33}=[U_{33\cdot3}-U_{33\cdot13}W_{13}-U_{33\cdot23}W_{23}]/U_{33\cdot33},$$

where

$$U_{ij\cdot k} = \sum_t x_{ijt}y_{kt},$$

$$U_{ij\cdot kl} = U_{kl\cdot ij} = \sum_t x_{ijt}x_{klt},$$

$$y_{kt} = p_{kt} + \Delta_{kt},$$

$$x_{iit} = p_{it}^2/\bar{W}_t,$$

$$x_{ijt} = p_{it}p_{jt}/\bar{W}_t \quad \text{for } i \neq j,$$

$$\bar{W}_t = \sum_i \sum_j p_{it}p_{jt}W_{ij},$$

and i, j, k, l range from 1 to 3.

The method of solution is to choose a starting set of W's in some manner, calculate the U's, and then solve the equations successively for the W's. For each equation the most recently obtained W's are used. We then return to the first equation, and continue in this way until the changes in successive W's decrease. We then use the final set of W's to calculate new U's, and repeat the process. This is continued until a new set of U's causes no change in the W's to the degree of accuracy required. There is room for judgment in deciding when to compute new U's and the process may be helped along by judicious guesses as to improved W's. The final solution will be the correct solution to Wright's normal equations, to the degree of approximation desired.

This method, applied to the averages of the two populations, gave the results in the first line of table 2. Then, in the belief that weighting might improve the result, each set of values was weighted by $1/p_{1t} + 1/p_{2t} + 1/p_{3t}$, giving a rough adjustment for the size of the random errors expected. Although the weights varied by a factor of 7.3, the estimated W's were changed by at most one unit in the second decimal place.

Inspection of the data suggested that equilibrium had been reached at about $p_1 = .80$, $p_2 = .15$, $p_3 = .05$, but the calculated W's would result in elimination of CH (see below). An attempt was accordingly made to force the W's to give this equilibrium, in order to see how much they would be changed. This was done by adding 100 additional "generations" with $p_1 = .80$, $p_2 = .15$ and $p_3 = .05$. Although the additional 100 generations should have swamped the original data, there was comparatively little change in the W's, and the new values still required the elimination of CH. This unpleasant result forced a reexamination of the estimation problem.

As stated above each sample contained 150 zygotes, or 300 chromosomes. The size of the population in the cage was at least 1,500 flies, or 3,000 chromosomes. Results of Prout (1954) indicate that the effective population size can then be taken to be large in comparison with sample size, and drift becomes relatively unimportant. Even when the frequency of CH is between .05 and .01, there will be 150 to 30 CH chromosomes present, and selection pressure will be the primary factor in causing changes in gene frequency.

The difference method outlined above, considers each pair of successive samples, and hence each Δ, independently of all the others. With the set of W's in the

first line of table 2, and $p_1 = .80$, $p_2 = .15$, $p_3 = .05$, the change in one generation is only to $p_1 = .813$, $p_2 = .149$, $p_3 = .038$. Evidently the estimated W's by this method are mainly influenced by the early part of the experiment, when changes in frequency are large and severely restrict the range of possible W's. On the other hand, a set of 100 Δ's, all equal to zero, with the above starting p's, is accounted for nearly as well by the given set of W's as by any other. If, however, we imagine 100 *successive* generations with no change in the p's, there would certainly be a real equilibrium and this set of W's is impossible since it would certainly lead to complete or nearly complete loss of CH long before 100 generations. This defect in this method of estimation is a serious one, since it makes it futile to try to learn whether a cage will reach equilibrium, even by the obvious method of continuing to observe the cage for a long period of time.

What is needed is a method of estimation which will, first, consider the observations in their proper sequence and, second, give them their proper weights. The method of minimum chi-square meets both these requirements. The procedure is as follows. Starting with a given set of W's, and the given initial gene frequencies, we calculate the successive theoretical frequencies for (in this case) 15 generations. For computational purposes, the most convenient formula for calculating the frequencies after one generation, $p_{i,\,t+g}$, starting from $p_{i,\,t}$, is

$$\begin{aligned} Z_1 &= (W_{11}p_1 + W_{12}p_2 + W_{13}p_3)p_1, \\ Z_2 &= (W_{12}p_1 + W_{22}p_2 + W_{23}p_3)p_2, \\ Z_3 &= (W_{13}p_1 + W_{23}p_2 + W_{33}p_3)p_3, \end{aligned} \tag{2}$$

$$\begin{aligned} p_{1,\,t+g} &= Z_1/(Z_1 + Z_2 + Z_3), \\ p_{2,\,t+g} &= Z_2/(Z_1 + Z_2 + Z_3), \\ p_{3,\,t+g} &= Z_3/(Z_1 + Z_2 + Z_3). \end{aligned}$$

Successive generations are obtained by repeated application of the formula. Then by numerical or graphical interpolation we calculate the theoretical values of p at the times the various samples were taken. Next chi-square is calculated for the differences between the observed and the calculated frequencies. Various sets of W's are tried until a set is found which gives the smallest possible chi-square. In this process the sizes of the various contributions to chi-square and the signs of the corresponding differences give clues as to the direction and amount to change the W's, but the method is still very laborious and of a trial and error nature. It is important to have a good first guess, and for this purpose the difference method estimate is suitable.

Although the difference method involves much computation, it is a constructive method, while it would be almost hopeless to apply the minimum chi-square method without a reasonable first estimate. The method of minimum chi-square applied to the averages of the

TABLE 2. *Various estimates of the adaptive values of the six karyotypes*

Set No.	Source and method	Homozygotes			Heterozygotes		
		ST/ST	AR/AR	CH/CH	ST/AR	ST/CH	AR/CH
1	Population A and B, difference method	0.83	0	0.43	1.00	0.67	0.60
2	Population A and B, minimum chi-square	0.83	0.15	0.36	1.00	0.77	0.62
3	Population A, minimum chi-square	0.83	0.20	0.36	1.00	0.74	0.59
4	Population B, minimum chi-square	0.83	0.14	0.36	1.00	0.80	0.62
5	Populations A and B, first 105 days minimum chi-square	0.94	0.06	0.51	1.00	0.48	0.52
6	Estimates based on earlier material	0.33	0.04	0.16	1.00	0.77	0.55

two populations gives the estimates in the second line of table 2, although it is possible that some slight improvement could still be made. The corresponding chi-square is 46.78. The initial p's are known nearly exactly, and there are no computed values for comparison; each of the 9 samples has two independent p's, giving a total of 18 degrees of freedom. Since 5 W's must be estimated from the data, 5 degrees of freedom are lost, giving 13 degrees of freedom for testing agreement of the data with the theory. For 13 degrees of freedom $\chi^2 = 46.78$ is highly significant. The poorness of the fit is due mainly to the erratic nature of the observed values, and could not be much improved. On the other hand, the W's given by the difference method give a much worse chi-squaref o about 100.

In an effort to find the effect of sampling error on the calculated W's the minimum chi-square method was applied separately to populations A and B. The resulting W's, shown in table 2 are in quite good agreement. The corresponding chi-squares, again with 13 degrees of freedom, are 32.7 for population A and 28.5 for population B. These are still highly significant, but the fact they are smaller than that for the average of the two populations (which is based on 600 chromosomes instead of 300) reinforces the impression that in addition to sampling error there are erratic fluctuations in the gene frequencies in the populations. These are much larger than could be accounted for by genetic random drift, but might be due to random fluctuations in selection pressure. Unpublished data of Louis Levine strongly suggests that

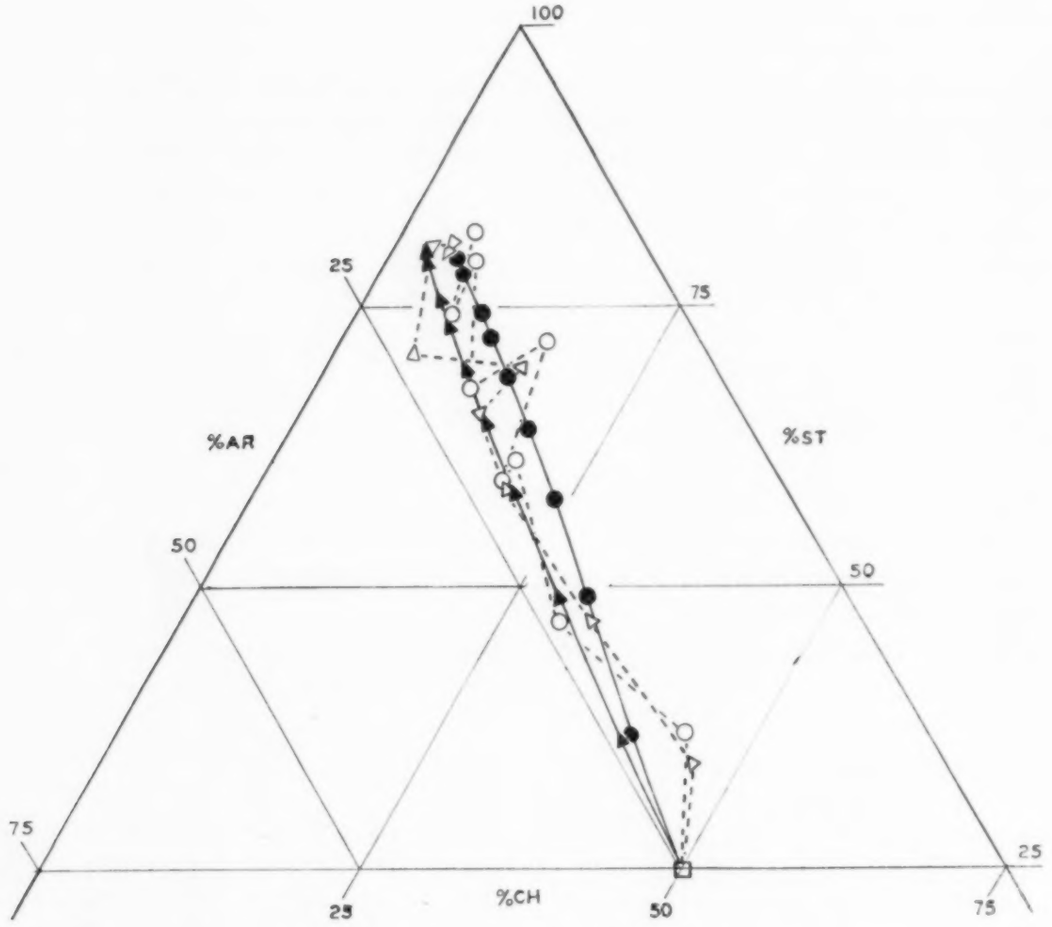


FIG. 1. Observed changes in gene frequencies and predicted changes on basis of minimum chi-square estimates of adaptive values. Triangles population A, circles population B. Broken lines with white symbols observed, solid lines with black symbols predicted values.

such fluctuations occur, due perhaps to changes in the environment in which the cages are kept. The observed and predicted values for populations A and B are shown in figure 1. Except for the erratic fluctuations the agreement is quite good.

The method of minimum chi-square is known to be efficient, and essentially equivalent to the method of maximum likelihood. The particular application here is valid if there is no genetic drift and the W's are constant. We have given reasons for considering drift of negligible importance in these experiments. In this connection it should be noted that the amount of drift probably present could accumulate and become important over 14 generations if we were dealing with adaptively neutral chromosomes, but selection pressures of the magnitude found here act as a restoring force and would keep the effect of drift negligible. Accordingly, the method of minimum chi-square gives us that set of constant W's that best fits the observations.

If the W's do in fact vary erratically, very little can be done, since they cannot be estimated from one or two samples. In fact each pair t_1, t_2 gives two independent Δ's. Since there are five W's to estimate, a minimum of three such pairs, or a minimum of four successive values of t are needed to estimate all the W's. If, now, the W's vary systematically as functions of the gene frequencies, as suggested above, this should be detectable by estimating them separately from the earlier and the later generations. The minimum chi-square estimate for the initial frequencies and first three samples for the average of the two populations is given in table 2. The W's differ, as expected, from those based on all the data. Attempts to find W's for the period from 105 days to the end of the experiment were unsuccessful. The random fluctuations for these later periods were too large in comparison with the directed changes to allow of any accuracy in estimation, and the results were unsatisfactory.

Further experiments are now under way to show the effect of gene frequencies on the adaptive values.

Condition for Equilibrium of Three Gene Alleles or Gene Arrangements

The theory of selection with more than two alleles has been considered by Sewall Wright in several papers, particularly in Wright (1949). Here we will consider certain aspects of the theory for three alleles in more detail. The adaptive values of the karyotypes will be supposed to be constant, and the population to be infinite. The state of a population at any time may be symbolized by a point on a triangular diagram, such as in figure 1. On this diagram there will be stable points which are points of neutral equilibrium, where no selective forces act. These include the three vertices, and also, if certain of the W's are equal, one side, or two sides, or the entire diagram. In general, neutral equilibrium is of little interest. There may also be points of stable equilibrium. A point will be called a point of absolute stable single, double or triple equilibrium if it is at a vertex, or a side, or in the interior of the triangle respectively, and if populations located at neighboring interior points tend to it as a limit at infinite time. A point will be called a point of conditional stable single or double equilibrium if the population tends toward it from neighboring points on one of the sides, but moves away from it from neighboring interior points. A point will be called a point of unstable triple or double equilibrium if it is a stable point, but the population moves away from it from every neighboring point. Examples of neutral equilibrium are obvious. Examples of the other types will be given below.

The location of a point of triple equilibrium is found by setting $\Delta_1 = \Delta_2 = \Delta_3 = 0$ and solving for the p's. The solution can be given in various forms,

such as equations (42) and (43) in Wright and Dobzhansky (1946). A convenient form is

$$
\begin{aligned}
a &= W_{12} - W_{11}, \quad b = W_{12} - W_{22}, \\
c &= W_{12} - W_{23}, \quad d = W_{13} - W_{11}, \\
e &= W_{13} - W_{33}, \quad f = W_{13} - W_{23}, \\
g_1 &= be - cf, \\
g_2 &= ae - df, \\
g_3 &= bd - ac, \\
\bar{p}_1 &= g_1/(g_1 + g_2 + g_3), \\
\bar{p}_2 &= g_2/(g_1 + g_2 + g_3), \\
\bar{p}_3 &= g_3/(g_1 + g_2 + g_3).
\end{aligned} \tag{3}
$$

The location of a point of double equilibrium is given by

$$
\begin{aligned}
\bar{p}_i &= (W_{ij} - W_{jj})/(2W_{ij} - W_{ii} - W_{jj}), \\
\bar{p}_j &= (W_{ij} - W_{ii})/(2W_{ij} - W_{ii} - W_{jj}),
\end{aligned} \tag{4}
$$

where only the ith and jth alleles are present.

For the case of two alleles a necessary and sufficient condition for stable equilibrium is W_{ij} greater than both W_{ii} and W_{jj}, and the necessary and sufficient condition for unstable equilibrium is W_{ij} less than both W_{ii} and W_{jj}. For the case of three alleles a necessary and sufficient condition for triple equilibrium is, by definition, $\bar{p}_1 > 0$, $\bar{p}_2 > 0$, $\bar{p}_3 > 0$. An unsuccessful attempt was made to find another condition with a more intuitive meaning in terms of the W's. At first it seemed that there would be stable equilibrium under condition 1, namely if each heterozygote was better than all the homozygotes. The following simple result shows that this is insufficient. If $W_{11} = W_{22} = W_{33} = 0$, equation (3) reduces to

$$
\begin{aligned}
g_1 &= W_{23}(W_{12} + W_{13} - W_{23}), \\
g_2 &= W_{13}(W_{12} + W_{23} - W_{13}), \\
g_3 &= W_{12}(W_{13} + W_{23} - W_{12}).
\end{aligned} \tag{3'}
$$

Obviously the necessary and sufficient condition for triple equilibrium is condition 2: that each of the three W's for heterozygotes be less than the sum of the other two, and the equilibrium will then be stable. Unfortunately, when the homozygotes are not lethal this added condition is neither necessary nor sufficient, as the examples below show.

The effect of a given set of W's may be studied by calculating the $\bar{p}$'s of equation 3. If they are all positive, there is a triple equilibrium, and inspection will show whether it is stable or unstable. In case of doubt equation (2) may be applied to points near the equilibrium point. If there is an unstable triple equilibrium, there will be two or three stable points of equilibrium on the boundary, and the one reached will depend on the starting point. If one or two of the $\bar{p}$'s are negative (all three cannot be negative) some study is again needed to see which allele is eliminated most rapidly. Then equation (4) is applied to the remaining two alleles to see if there is a double equilibrium (which would necessarily be unconditional). If not, one allele eliminates the other two.

We now examine the estimates of the W's obtained from this experiment, and also some illustrative hypothetical sets of W's, for the nature of the equilibrium. The equilibrium values are given in table 3. All of the estimates for populations A and B in table 2 are in general agreement. Condition 1 does not hold, but condition 2 does. There is no triple equilibrium, $\bar{p}_3$ being negative. CH is eliminated and there is a stable double equilibrium with more ST than AR. There is a conditional stable double equilibrium with more CH than AR, and no stable double equilibrium with ST and CH. (Set 5 does give an unstable triple equilibrium, but it is so close to 100% CH as to be unimportant.)

Sewall Wright's estimates (Wright and Dobzhansky, 1946) for a different set of populations satisfy conditions 1 and 2. There is a stable triple equilibrium and three stable conditional double equilibria. Set 7 in table 3 represents one of

TABLE 3. *The frequencies of the different chromosomes at equilibria with different adaptive values*

Set No.	Adaptive values						Triple equilibria			Double equilibria					
	W_{11}	W_{22}	W_{33}	W_{12}	W_{13}	W_{23}	$\bar{p}_1$	$\bar{p}_2$	$\bar{p}_3$	$\bar{p}_1$	$\bar{p}_2$	$\bar{p}_1$	$\bar{p}_3$	$\bar{p}_2$	$\bar{p}_3$
1	.83	0	.43	1.00	.67	.60	.85	.15	0	.85	.15	1.00	0	.23	.77
2	.83	.15	.36	1.00	.77	.62	.83	.17	0	.83	.17	1.00	0	.36	.64
3	.83	.20	.36	1.00	.74	.59	.82	.17	0	.82	.17	1.00	0	.37	.63
4	.83	.14	.36	1.00	.80	.62	.83	.16	0	.83	.16	1.00	0	.35	.65
5	.94	.06	.51	1.00	.48	.52	.94	.06	0	.94	.06	.06*	.94*	.02	.98
6	.33	.04	.16	1.00	.77	.55	.53	.34	.13	.59	.41	.58	.42	.43	.57
7	.83	0	1.22	1.00	.54	.62	.57*	.12*	.31*	.85	.15	.70*	.30*	0	1.00
8	.90	.05	.05	1.40	1.20	.80	.70	.24	.08	.73	.27	.79	.21	.50	.50
9	.50	.30	.30	1.30	.90	.70	5/9	4/9	0	5/9	4/9	.60	.40	.50	.50
10	0	0	1.40	3.00	1.40	1.30	.14	.12	.74	.50	.50	0	1.00	0	1.00
11	1.00	1.00	.90	1.00	.90	.90	‡	‡	0	‡	‡	1.00	0	1.00	0

* unstable equilibrium
‡ neutral equilibrium

the abortive attempts to get adaptive values for the samples from 105 days on. Condition 1 is not satisfied, conditon 2 is. There is a point of unstable triple equilibrium. Depending on the starting point the stable equilibrium is AR and ST both eliminated, or CH eliminated with more ST than AR. Sets 8 through 11 in table 3 represent hypothetical values. Set 8 does not satisfy condition 1, yet there is a stable triple equilibrium and three stable double equilibria. Set 9 satisfies both conditions 1 and 2, yet there is no triple equilibrium. Set 10 satisfies neither condition 1 nor condition 2, yet there is a stable triple equilibrium. Thus condition 1 and condition 2 are neither necessary nor sufficient for triple equilibrium.

Finally set 11 presents a new complication. Equations 4 break down, giving $g_1 = g_2 = g_3 = 0$, and the $\bar{p}$'s are undefined. Further study shows that allele 3 is eliminated and 1 and 2 form a neutral equilibrium. The actual course of events would be for the relative proportions of 1 and 2 to remain unchanged while 3 is lost; on the diagram the point would move directly away from the third vertex.

GENE FLOW DIAGRAMS

Figure 1 shows the theoretical course of events when the adaptive values are the ones given by minimum chi-square for populations A and B, but only for the combination of gene frequencies used in this experiment. A more general picture of the consequences of a given set of W's is given by the diagram in figure 2. Here a number of starting points are chosen, systematically distributed over the triangle diagram, and for each the result of one generation of selection is calculated. A line is then drawn between the initial and final values, with an arrowhead to show the direction of change. The final diagram resembles the flow diagrams of hydrodynamics and will be called a gene flow diagram. If the arrows are dense enough one can get a rough idea of the path followed from every starting value, and the approximate number of generations required. All such diagrams have certain features in common. As the arrows get close to the boundaries, or to an interior point of equilibrium, they get shorter and shorter, an infinite time being theoretically required to actually reach them (or to leave them once there). The arrows converge upon points of

stable equilibrium and diverge from points of unstable equilibrium.

Figures 2 and 3 give the gene flow diagrams for the W's calculated by minimum chi-square from the averages of the two populations for the entire experiment and for the first 105 days respectively. For comparison with a case where there is a stable triple equilibrium, figure 4 gives the flow diagram for the W's calculated by Wright and Dobzhansky (1946). Figure 5 is an example of unstable triple equilibrium based on the W's of set 7 in table 3. For several starting values a series of generations have been calculated here, to show the sensitivity of the outcome on the starting value.

Inspection of the flow diagrams suggests another question. If the p's change, but the ratio p_2/p_3 remains constant, the arrow will point either straight towards or straight away from the first vertex. For what initial values of the p's will this happen? Setting $Z_2/Z_3 = p_2/p_3$ in equation (2), we obtain the condition

$$p_1W_{12} + p_2W_{22} + p_3W_{23} = p_1W_{13} + p_2W_{23} + p_3W_{33}. \tag{5}$$

This is the equation of a straight line on the triangle diagram. Setting $p_3 = 1 - p_1 - p_2$ and solving for p_2, we have

$$p_2 = \frac{W_{23} - W_{33} + (W_{12} + W_{33} - W_{13} - W_{23})p_1}{2W_{23} - W_{22} - W_{33}}, \tag{6}$$

from which the line may easily be drawn. Similarly the ratio p_3/p_1 remains constant if

$$p_3 = \frac{W_{13} - W_{11} + (W_{23} + W_{11} - W_{12} - W_{13})p_2}{2W_{13} - W_{11} - W_{33}}, \tag{7}$$

and the ratio p_1/p_2 remains constant if

$$p_1 = \frac{W_{12} - W_{22} + (W_{13} + W_{22} - W_{12} - W_{23})p_3}{2W_{12} - W_{11} - W_{22}}. \tag{8}$$

Arrows starting on the lines given by equations (6), (7), and (8) move either directly towards or directly away from vertices 1, 2, and 3 respectively, and we will refer to these lines as lines I, II and III.

Let us now consider line I in some detail. It can easily be shown that for a given value of p_1, if the value of p_2 is less than that given by equation (6), the ratio p_2/p_3 will increase; i.e., for a starting point above and to the right of line I the arrow will be deflected toward vertex 2 or away from vertex 3. For points below and to the left of line I the reverse is true. If, for all p_1 between zero and one, p_2 calculated from equation (6) is negative, line I does not exist, and p_2 always decreases relative to p_3. If, for all p_1 between zero and one, $p_1 + p_2$ is greater than one, line I does not exist and p_2 always increases relative to p_3. Since, for every starting point on line I, p_2/p_3 remains constant, if this line crosses the boundary $p_3 = 0$ the intersection will be a point of stable or unstable double equilibrium. Conversely, if a point of double equilibrium between p_2 and p_3 exists, line I will exist and pass through the equilibrium point. However, line I may exist without crossing the boundary $p_3 = 0$ when no double equilibrium exists. Similar results hold for lines II and III.

If lines I and II intersect within the triangle, at the point of intersection p_2/p_3 remains constant and p_1/p_3 remains constant. Hence, at this point

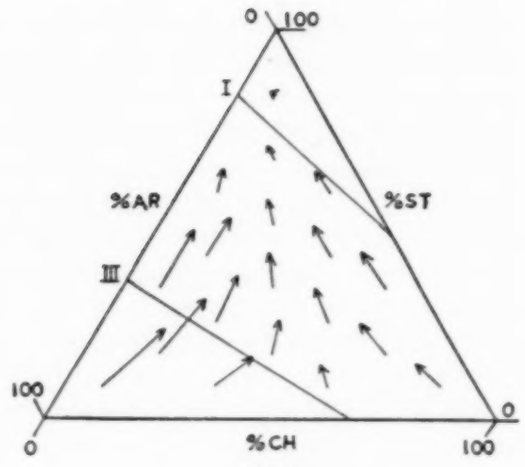


FIG. 2

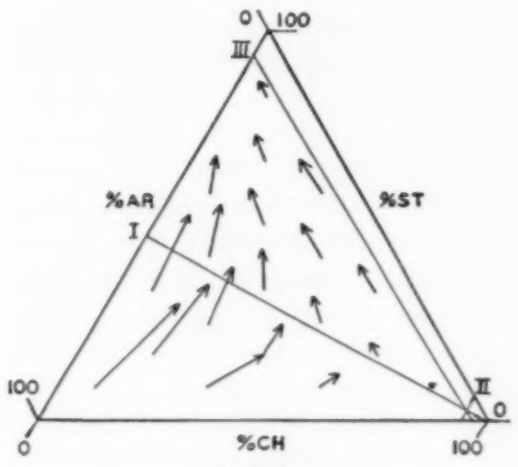


FIG. 3

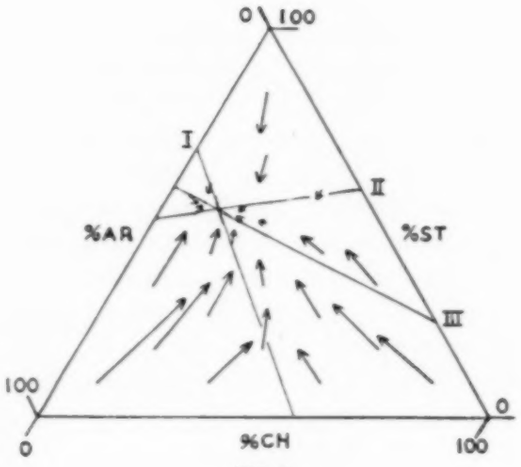


FIG. 4

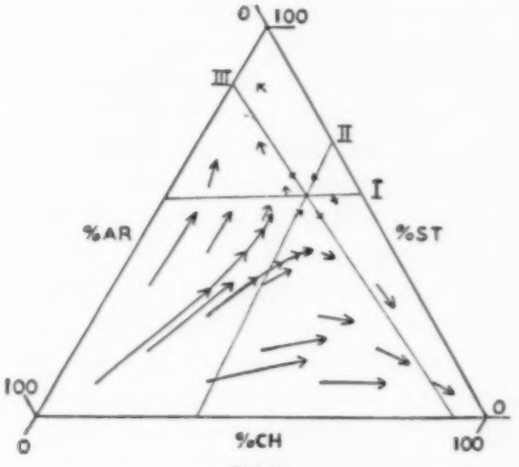


FIG. 5

FIGS. 2–5. Gene flow diagrams for sets of adaptive values 2, 5, 6, and 7 respectively of tables 2 and 3. Each arrow goes from an arbitrary starting value to the gene frequencies resulting from one generation of selection. Intersection of lines I, II, III is point of stable equilibrium in figure 4, and unstable equilibrium in figures 3 and 5. Further explanation in text.

p_1/p_2 also remains constant, or $p_1 = p_2 = p_3$. Hence line III also passes through the point and it is a point of triple equilibrium. Conversely, if there is a point of triple equilibrium all three lines exist and intersect at it.

Consequently, all questions about equilibrium can be answered by drawing whichever one of lines I, II, and III exists. Since this is little more labor than the direct investigation of equilibrium given above, and since the lines give additional information, this is probably the preferred method of investigation. From the lines, a general idea of the directions of gene flow may be obtained, although direct calculations are needed to determine its speed.

Figures 2 to 5 include lines I, II, and III. In figure 2 line II does not exist, and p_3/p_1 always decreases. Figures 4 and 5 have arrows starting on each line near their intersection to show the peculiar nature of the gene flow near a point of triple equilibrium. One might at first imagine that the population point moves more or less directly toward a stable equilibrium point. Actually it often moves quite obliquely. Indeed study shows that for figure 4, regardless of the starting point the ultimate path of approach lies within one of the two angles formed by the intersection of lines II and III. Finally, inspection shows that arrows starting on a given line on opposite sides of a point of triple equilibrium

point in nearly opposite directions. The general results above show that this will always be true.

Dependence of the Adaptive Values on the Composition of the Populations

Though obviously lacking in precision, the estimates of the adaptive values of the different karyotypes shown in table 2 agree in showing certain significant relationships. Thus, the ST/AR heterozygotes are the fittest karyotype, followed by the ST/ST homozygotes. The lowest fitness is shown by AR/AR homozygotes, CH/CH being intermediate between ST/ST and AR/AR. Most of these relationships appear even in Wright's old estimates, made on the basis of old data, the preliminary nature of which was clearly realized (Wright and Dobzhansky, 1946).

The figures summarized in table 2 permit making certain deductions which can be tested experimentally. The adaptive values of the AR and CH homozygotes and AR/CH heterozygotes very clearly form the series AR/CH > CH/CH > AR/AR. This being the case, populations containing only AR and CH chromosomes must reach equilibria at which CH should be considerably more frequent than AR. Exactly the opposite result, i.e., a greater frequency of AR than of CH, has, however, been observed by Wright and Dobzhansky (1946), Dobzhansky (1948, 1947), and Louis Levine (unpublished data). In populations with only two gene arrangements, AR and CH, the hierarchy of the adaptive values is, consequently AR/CH > AR/AR > CH/CH. In populations containing the three gene arrangements the ST/ST homozygotes are more fit than the ST/CH and CH/CH karyotypes (ST/ST > ST/CH > CH/CH, see table 2). This leads to the prediction that in populations in which only these two gene arrangements are present no equilibrium should be reached, and ST chromosomes should replace CH entirely. This prediction is again contrary to fact: Equilibria with a predominance of ST over CH have been observed by Wright and Dobzhansky (1946), Dobzhansky (1947, 1948), da Cunha (1951), and Dobzhansky and Pavlovsky (1953). Only Epling, Mitchell and Mattoni (1953) thought that CH chromosomes were in the process of elimination in some of their experiments. This claim, even if confirmed, would be irrelevant here, being based on experiments conducted in an environment inadequately described but in all probability different from that in our populations. The sensitivity of the adaptive values of the karyotypes to environmental modifications has been known for some time (Wright and Dobzhansky, 1946; Dobzhansky, 1948; da Cunha, 1951). In populations in which only ST and CH chromosomes are present, the adaptive values form the series ST/CH > ST/ST > CH/ST, in the environments of our experiments.

The discrepancies observed can have but one explanation. The adaptive value of a genotype in a given environment depends upon the properties of that genotype as well as upon those of the other genotypes present in the same environment. In a way, the foregoing statement is a tautology: The environment of an organism may be altered by the proximity of other organisms. The concept of environment must certainly be understood broadly, including not only the physical but also the biotic variables. The AR/AR homozygotes are superior in fitness to CH/CH in populations containing no ST chromosomes, but the relationship is reversed when ST chromosomes are present. Similarly, the relative adaptive values of ST/CH and ST/ST depend upon the presence or absence of AR chromosomes in the same population.

The fact that the adaptive values calculated for the first 105 days differ from those calculated for the whole experiment is now understandable. A

glance at table 1 suffices to show that some of the karyotypes underwent great changes in frequencies during the experiments. Since the adaptive value of a karyotype may depend on what other karyotypes are present in the same environment, it is not unexpected that the selective pressures in the populations A and B have not remained constant with the progress of selection. Thus, it appears that the fitness of the ST/ST homozygotes was higher in these populations at the beginning of the experiments, when this karyotype was rare, than towards the end, when it became frequent (table 2). The figures also suggest that the adaptive values of the AR/CH and ST/CH heterozygotes increased slightly as these karyotypes became rare in the populations. It would be premature at this time to draw the inference that the fitness of a karyotype is inversely related to its frequency in the population, although the figures in table 2 (except for CH/CH) suggest such a relationship.

Architecture of the Gene Pool

Recent advances in population genetics tend to emphasize the delicate adjustments which exist between many components of the gene pool of a Mendelian population. Linked gene complexes which occur in such populations are often, perhaps even in a majority of cases, deleterious when homozygous, but highly fit in heterozygous combinations with other gene complexes found in the same gene pool (Wallace and Madden, 1953; Dobzhansky and Spassky, 1953, 1954). A similar mutual adjustment exists also between the gene arrangements responsible for the balanced polymorphism observed in many populations of Drosophila, the structural heterozygotes having a net advantage in adaptive value over the homozygotes.

Dobzhansky and Levene (1948) found that inversion heterozygotes are, on the average, slightly more, and inversion homozygotes less, frequent in natural populations of *D. pseudoobscura* than expected on the basis of the binomial square rule. It follows that, considering the populations of all the localities studied as a whole, there is an over-all tendency for differential survival favoring the heterozygotes. A similar situation is indicated for *D. willistoni* (da Cunha, 1953). The sensitivity of the adaptive values of the karyotypes in natural polymorphic populations makes, however, the magnitude and the direction of the selection pressure vary in different localities, at different seasons, and even in the two sexes. Apart from *D. pseudoobscura*, such variations have been observed in *D. robusta* (Levitan, 1951 and unpublished data) and in *D. polymorpha* (da Cunha, 1949).

Epling, Mitchell, and Mattoni (1953) found that, in *D. pseudoobscura* on Mount San Jacinto, the deviations from the frequencies demanded by the binomial square rule affect at different seasons different zygotic classes. They concluded that inversion heterozygotes in this species are not "adaptively superior to the corresponding homozygotes." Differential survival between the egg and the adult stages should not be confused, however, with differences in adaptive values. A less viable genotype may be superior in adaptive value to a more viable genotype, and vice versa. The viability is not necessarily proportional to fecundity, longevity, sexual activity, and other variables which, together with the viability, determine the adaptive value of a genotype or a karyotpye. The adaptive values can not be deduced from the kind of data considered by Epling and his colleagues. Da Cunha (1949) found a balanced polymorphism in *D. polymorpha* despite a systematic deficiency in the viability of the heterozygotes. The degree of adaptedness of karyotypes of *D. pseudoobscura* varies at different seasons and in the different facies of the environment which the species inhabits.

This is assuredly no evidence that the persistence of the karyotypes in the population is not due to balanced polymorphism.

The sensitivity of the adaptive values of the karyotypes which occur in polymorphic populations of *D. pseudoobscura* to environmental factors is indeed remarkable. Moreover, this sensitivity is itself an adaptive trait which permits the adaptedness of the populations to reach a high degree of precision. It should be kept in mind that the experiments described in this article have been made at 25° C. At 16° C. the adaptive values of these karyotypes are very near equality (Wright and Dobzhansky, 1946; Dobzhansky, 1949). Yet, Spiess (1950) discovered that in the closely related *D. persimilis* the karyotypes have different adaptive values at 16° C. but tend towards equality at 25° C. Again the adaptive value of a karyotype depends on the species of microorganisms which the flies use for food (da Cunha, 1951 and unpublished experiments of Dobzhansky and Spassky). Finally, the data presented in this article show that the adaptive value of a karyotype is modified by the presence of individuals with other karyotypes in the same environment.

Summary

Experimental populations of *Drosophila pseudoobscura* were set up in which three different gene arrangements (ST, AR, and CH) were present among the third chromosomes. Six karyotypes are found in such populations—the structural homozygotes ST/ST, AR/AR, and CH/CH, and the heterozygotes ST/AR, ST/CH, and AR/CH. The adaptive values of these karyotypes were estimated from the changes which took place in the populations under the influence of natural selection. The structural heterozygotes were for the most part adaptively superior to the corresponding homozygotes, i.e., showed heterosis. The adaptive values of the karyotypes were shown, however, to depend not only on the physical environment and the nutritional conditions but also on what other karyotypes were present in the same populations. An improved method for estimating adaptive values was developed, and the theory of the behavior of populations with three karyotypes is discussed.

Acknowledgments

The authors are obligated to Mrs. T. D. Gidaspow for making most of the calculations needed to estimate the adaptive values of the karyotypes. Mr. Louis Levine determined the karyotypes in the sample taken when the populations were 245 days old (table 1). All other samples were scored by one of the authors (Th. Dobzhansky).

Literature Cited

da Cunha, A. B. 1949. Genetic analysis of the polymorphism of color pattern in *Drosophila polymorpha*. Evolution, **3**: 239–251.

——. 1951. Modification of the adaptive values of chromosomal types in *Drosophila pseudoobscura*. Evolution, **5**: 395–404.

——. 1953. Chromosomal inversions with sex-limited effects. Nature, **172**: 815–816.

Dobzhansky, Th. 1948. Genetics of natural populations. XVIII. Genetics, **33**: 588–602.

——. 1949. Observations and experiments on natural selection in *Drosophila*. Proc. 8th Internat. Congr. Genetics: 210–224.

—— and Levene, H. 1948. Genetics of natural populations. XVII. Genetics, **33**: 537–547.

—— ——. 1951. Development of heterosis through natural selection in experimental populations of *Drosophila pseudoobscura*. Amer. Natur., **85**: 247–264.

——, and O. Pavlovsky. 1953. Indeterminate outcome of certain experiments on *Drosophila* populations. Evolution, **7**: 198–210.

——, and B. Spassky. 1953. Genetics of natural populations. XXI. Genetics, **38**: 471–484.

—— ——. 1954. Genetics of natural populations. XXII. Genetics, **39** (in press).

Epling, C., D. F. Mitchell, and R. H. T. Mattoni. 1953. On the role of inversions in wild populations of *Drosophila pseudoobscura*. Evolution, **7**: 342–365.

LEVITAN, M. 1951. Selective differences between males and females of *Drosophila robusta*. Amer. Natur., **85**: 385–388.

PROUT, T. 1954. Genetic drift in irradiated experimental populations of *Drosophila melanogaster*. Genetics, **39** (in press).

SPIESS, E. 1950. Experimental populations of *Drosophila persimilis* from an altitudinal transect of the Sierra Nevada. Evolution, **4**: 14–33.

WALLACE, B., AND G. MADDEN. 1953. The frequencies of sub- and supervitals in experimental populations of *Drosophila melanogaster*. Genetics, **38**: 456–470.

WRIGHT, S. 1949. "Adaptation and selection," in Genetics, Paleontology, and Evolution, ed. by Jepsen, G. L., Simpson, G. G., and Mayr, E. Princeton.

——, AND TH. DOBZHANSKY. 1946. Genetics of natural populations. XII. Genetics, **31**: 125–156.

—— ——. 1947. Genetics of natural populations. XIV. Genetics, **32**: 142–160.

AN EXTREME FORM OF CHIASMA LOCALIZATION IN A SPECIES OF *BRYODEMA* (ORTHOPTERA, ACRIDIDAE)

M. J. D. White

Division of Plant Industry, C.S.I.R.O., Canberra, Australia

Received, April 15, 1954

Introduction

In previous papers (White, 1949, 1950, 1951a, b, c, d, e) the peculiar mechanism of structural heterozygosity which exists in certain species of the North American grasshopper genus *Trimerotropis* and in the related genera *Circotettix* and *Aerochoreutes* has been discussed. These three genera may be referred to as the group Trimerotropi, a taxonomic entity which is confined to North America, except for two species of *Trimerotropis* which have penetrated to South America, doubtless at a geologically rather recent date.

It has long been believed by taxonomists that the Trimerotropi, and more especially the genera *Circotettix* and *Aerochoreutes,* are closely related to the palaearctic group Bryodemae. This view was expressed by Rehn (1921) when creating the genus *Aerochoreutes* and by Bey-Bienko (1930) when monographing the Bryodemae (which include the genera *Bryodema, Angaracris, Uvaroviola,* and *Compsorhipis* from Eastern Europe, U.S.S.R., Tibet, Mongolia, and N. China). In fact the latter author regards *Circotettix* and *Aerochoreutes* simply as nearctic offshoots of the Bryodemae, without discussing their evident relationship to the large and rather heterogeneous assemblage of species currently included in the genus *Trimerotropis.*

In view of this generally-accepted systematic relationship between the Trimerotropines (or some of them, at any rate) and the Bryodemae, it seemed desirable to make a cytological study of some representatives of the latter group. It will be appreciated that it is not easy, under present conditions, to obtain material of the Bryodemae. However, through the great kindness of Dr. W. Jacobs (University of Munich), fixed testes of ten individuals of *Bryodema tuberculatum bavaricum* Zacher collected by him in the mountains of Bavaria were obtained. Since the cytology of this form is radically different from that of any Trimerotropine and presents certain features of unusual interest, it seems worth description.

Observations

Spermatogonial metaphases of *B. tuberculatum bavaricum* (fig. 1a) show 23 acrocentric chromosomes (i.e. elements consisting of a long arm and a very minute one, separated by the centromere). The X-chromosome is easily distinguishable on account of its negative heteropycnosis at this stage. The 11 pairs of autosomes form a graded series in respect to length, but two pairs are markedly smaller than the others, and of these, the smallest, No. 11, is easily distinguishable from the next, No. 10.

It will be convenient to begin our account of meiosis with a description of the first metaphase stage, reserving discussion of the prophase stages until later. The first metaphases (fig. 2) are extraordinarily similar to those of the grasshoppers of the genus *Stethophyma* (= *Mecostethus*) figured and described by Janssens, McClung, White, and Callan (for references see White, 1954). The 11 autosomal bivalents show a very low chiasma frequency and an extreme degree of chiasma localization. Most of these bivalents appear in polar view as large, wide-open V's. Actually, by focus-

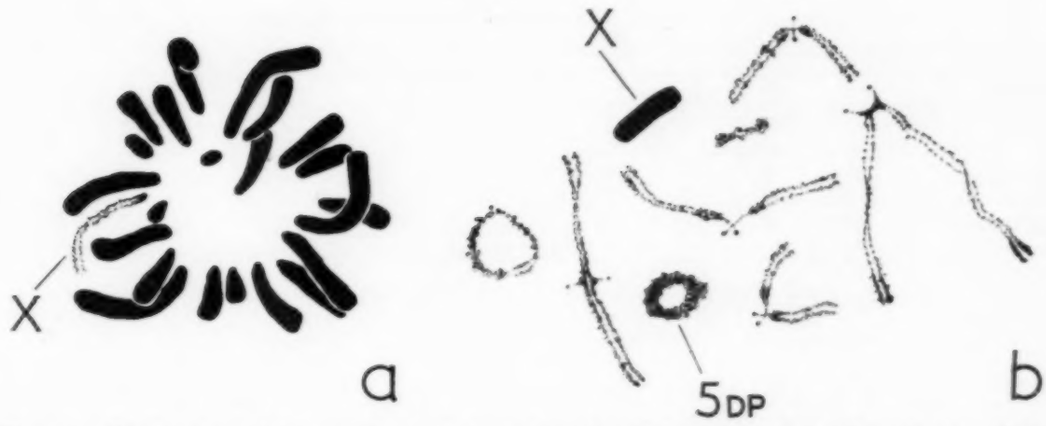


FIG. 1. Spermatogonial metaphase (a) and early diplotene (b) in *Bryodema*. Not all the eleven bivalents are shown in the latter, which shows the X, six bivalents with a single chiasma, and two with two chiasmata. 5_{DP} the fifth bivalent with a distal and a proximal chiasma.

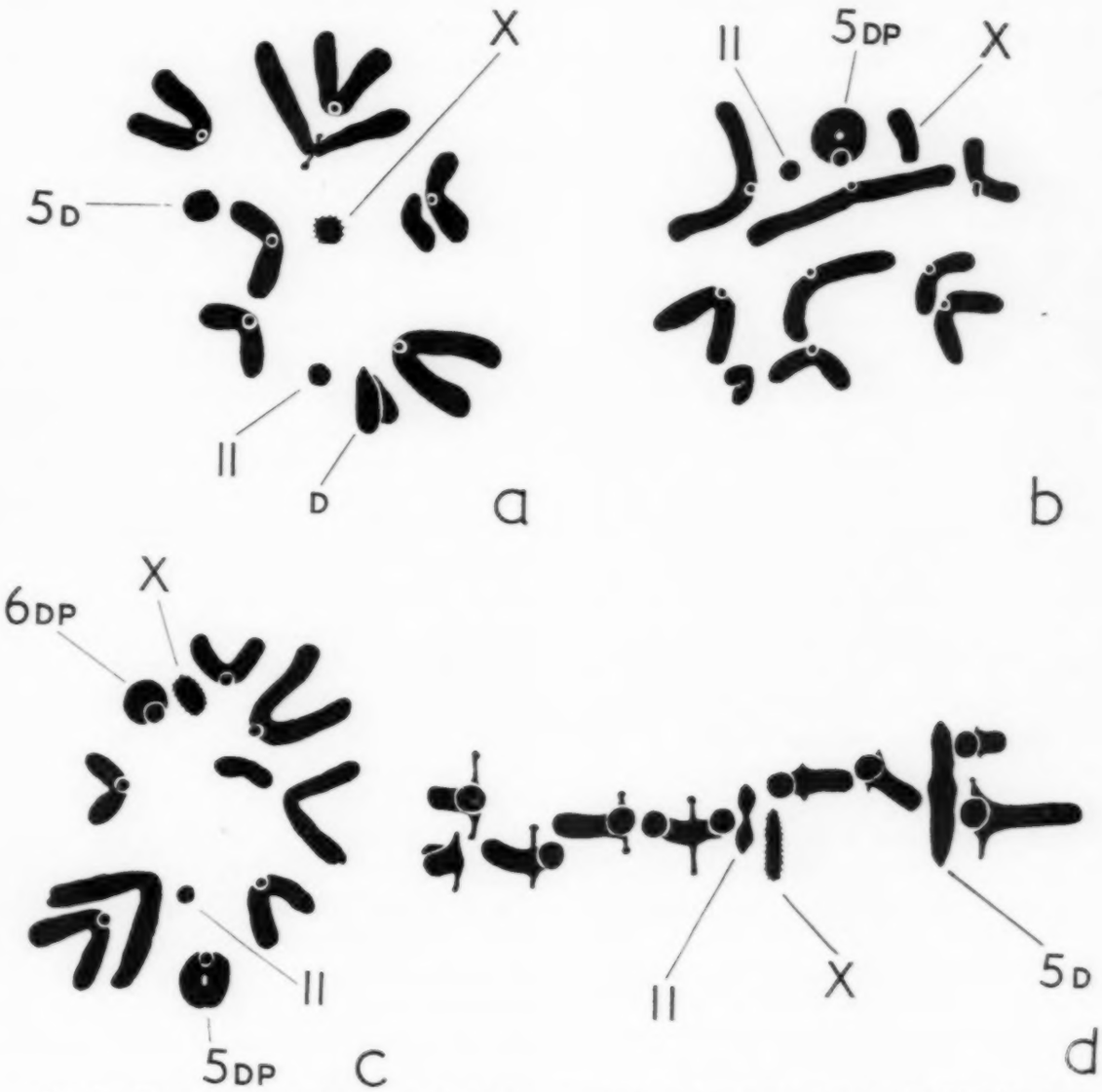


FIG. 2. Four first metaphases; *a*, *b* and *c* in polar view, *d* in side view 5_D, the fifth bivalent with a single distal chiasma; 5_{DP}, the same with a distal and a proximal chiasma; 6_{DP}, the sixth bivalent with two chiasmata; D, a bivalent which probably has the proximal chiasma in the "short arm."

TABLE 1. *Nuclei with various numbers of chiasmata*

Individual	A	B	C	D		E				F			G
Cyst No.	–	–	–	1	2	1	2	3	4	1	2	3	–
11 chiasmata	1	9	–	8	10	1*	–	–	–	18	23	13	11
12 chiasmata	5†	2	9	–	–	10	2	7	8	3‡	1‡	2	8§
13 chiasmata	–	–	–	–	–	6	–	4	2	–	–	–	–
14 chiasmata	–	• –	–	–	–	1	–	–	2	–	–	–	–
Total	6	11	9	18		43				60			19

* This cell falls in the 11-chiasmata category because it showed 2 univalents—otherwise it would have been included in the 12-chiasmata category since it had 1 ring bivalent.

† In 4 of these cells the ring bivalent was No. 6 rather than No. 5 and No. 5 had only a distal chiasma.

‡ In 1 of these cells the ring bivalent was No. 6 rather than No. 5 and No. 5 had only a distal chiasma.

§ In 3 of these cells the ring bivalent was No. 6 rather than No. 5 and No. 5 had only a distal chiasma.

ing up and down, one can see that they are really four-armed structures, two very short vertical limbs arising at the point of junction of the much longer horizontal limbs. The vertical limbs consist of the "short arm," the centromere, and a small proximal part of the long arm.

Such bivalents possess a single chiasma in the long arm, situated very close to the centromere. In some instances, where the "vertical" limbs are too small to be seen, the chiasma may be actually adjacent to the centromere; in other cases, it lies a little distance away from it but still in its immediate neighborhood. If we were to take the relative lengths of the "vertical" and "horizontal" limbs in such bivalents as an indication of the position of the chiasma along the chromonema, we might conclude that the chiasma was invariably situated in the proximal tenth of the genetic chromosome. But if we make the same calculation on the basis of relative volumes rather than relative lengths (which seems more justifiable, the vertical arms being much more slender), we reach the conclusion that the chiasma is restricted to a much shorter section of the total chromosome length.

TABLE 2. *Chiasma frequency Distribution of bivalent No. 5*

Chiasmata	Individual A	B	C	D	E	F	G
Distal only	5	9	0	18	0	56	14
Proximal and Distal	1	2	9	0	43	4	5

Of the 11 bivalents, two do not conform to the above description. The smallest, No. 11, seems invariably to form a single distal chiasma (rather than a proximal one), so that at first metaphase it consists of two small ovoid bodies lying "vertically" one above the other. Another anomalous bivalent, which we have called No. 5, also invariably forms a distal chiasma. But in 64 out of 166 first metaphases studied (see table 2) this bivalent also possesses a proximal chiasma, i.e. it forms a small ring.

As a result of these regularities of chiasma formation, most first metaphases show either 11 or 12 chiasmata, the fifth chromosome pair being represented either by a vertical rod-bivalent (fig. 2d) or by a ring-bivalent. In some individuals, however, one or two bivalents other than No. 5, form both distal and proximal chiasmata (table 1).

An inspection of tables 1 and 2 reveals, in spite of the limited data, that there are significant differences in chiasma fre-

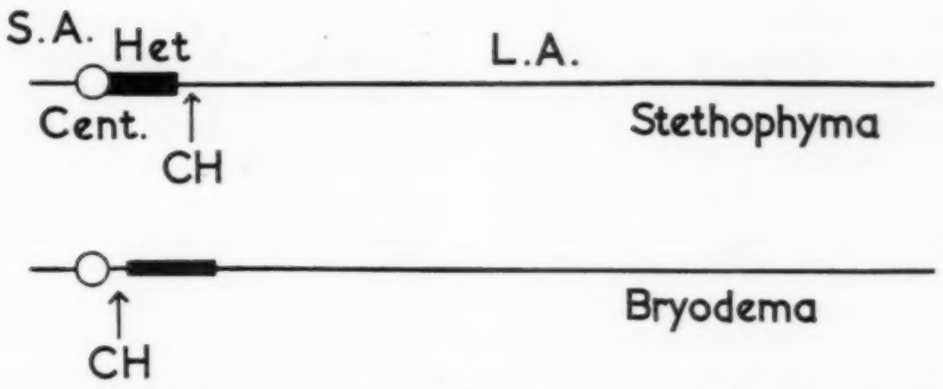


FIG. 3. Diagram showing the position of formation of the proximal chiasma (CH) in relation to the centromere (Cent.) and the proximal heterochromatin(Het) in *Stethophyma* and Bryodema. L.A., long arm; S.A., short arm.

quency between the individuals studied. Thus in individuals D and F chromosome 5 almost always forms a rod-bivalent with only one distal chiasma; while in individuals C and E it always possessed both a proximal and a distal chiasma. Whether these differences between individuals are due in the main to genetic or environmental causes is, of course, quite unknown. The very limited data on individuals D, E, and F suggest that there are no significant differences between the cysts of a single testis in regard to chiasma frequency.

The general appearance of the diplotene bivalents of *Bryodema* is shown in figure 1b. It will be seen that the X is strongly heteropycnotic at this stage. On the other hand, autosomal heterochromatin is nothing like as conspicuous as it is in *Stethophyma*. The 5th bivalent (i.e. the one which frequently forms a second chiasma) is, however, clearly heteropycnotic throughout a large part of its length and appears much thicker than the others during the diplotene stage. In the other autosomes slightly but definitely condensed proximal segments can be made out. These regions are in all cases distal to the proximal chiasma, i.e. the chiasma occurs *between* the centromere and the proximal heterochromatin. (See diagram, fig. 3.) This seems to be an important point of difference between *Bryodema* and *Stethophyma,* since in the latter the chiasma is formed *distal* to the proximal block of heterochromatin (White, 1936; Callan and Montalenti, 1947). The centromeres cannot, of course, be actually seen in these stained preparations of diplotene chromosomes, but the "short arms" on the far side of them show up very clearly as tiny, deep-staining "trabants." The difference in the relative positions of the chiasma and the heterochromatin in *Bryodema* and *Stethophyma* probably means that the position of the chiasma is fixed within even narrower limits in the former and is even closer to the centromere. It is possible that the proximal chiasmata in *Bryodema* are even closer to the centromeres at diplotene than at first metaphase, i.e. that a slight movement of the chiasmata away from the centromeres takes place between these stages.

No special study of pachytene or earlier prophase stages was undertaken, the sectioned material not being suitable for this purpose. Enough observations of pachytene nuclei were made, however, to convince us that Darlington's hypothesis that chiasma localization is due to incomplete or interrupted pairing does not apply in the present case, the pachytene bivalents being apparently completely paired from end to end.

DISCUSSION

Significance of chiasma localization

Some degree of chiasma localization is probably universal in organisms possessing

chiasmata at meiosis. It is, in fact, unlikely that any animal or plant has an entirely random distribution of crossing-over along the length of its chromosomes. Chiasma localization can, however, only be studied cytologically in species whose chromosomes are long enough at the relevant stages of meiosis so that the positions of the chiasmata can be determined with a sufficient degree of accuracy. In view of these considerations, it is not surprising that most studies of localization have been carried out on such organisms as Liliaceae (Darlington, 1935; Frankel, 1940), Urodeles (Callan, 1942; Wickbom, 1945), and grasshoppers (see White, 1954, for references to the earlier literature) in which the chromosomes are exceptionally large. Two main types of localization have generally been distinguished, *proximal* and *distal*. In the first the chiasmata are restricted to the neighborhood of the centromere, while in the second they are confined to short regions near the ends of the chromosomes.

Bryodema tuberculatum is probably the most extreme example of chiasma localization thus far known, although in many other species with small chromosomes and very low chiasma frequencies, the positions of the chiasmata may be equally restricted.

Such a rigid localization of chiasma formation to minute regions very close to the proximal and distal ends of acrocentric chromosomes represents, in effect, an almost complete suppression of intra-chromosomal genetic recombination. Chiasmata occur, but they are genetically ineffective. There can be very little doubt that if *Bryodema* were studied genetically it would be described as having "no crossing-over in the male," particularly since the minute "short arms" which would show crossing-over are probably heterochromatic and hence genetically inert.

In most of the more extreme examples of chiasma localization that have been studied (*Triturus palmatus* and *vulgaris*, *Stethophyma* spp., *Bryodema*) chiasma distribution in the female meiosis has not been investigated. For an understanding of the genetic and evolutionary significance of the whole phenomenon, the next step is surely a study of the oogenesis of some such form as *Bryodema* or *Stethophyma* to determine whether the distribution of chiasmata in the female is of the same type as in the male. As far as animals are concerned, almost the only evidence bearing on this point comes from cytogenetic work on the silkworm. It is well-known that in this insect there is no crossing-over in the female, but a moderate amount in the male (Tanaka, 1953). The figures of Maeda (1939) suggest that the chiasmata are strictly localized in the female, but more randomly distributed in the male. In the species of the plant genus *Fritillaria*, however, the same degree of localization occurs in the embryo-sac as in the pollen-mother-cell (Darlington and La Cour, 1941).

From all standpoints, there is a fundamental qualitative distinction between partial localization of chiasmata (in which they are formed with different frequencies in different parts of the chromosome, but in which no region has a zero frequency) and *absolute* localization (in which certain chromosomal regions have a zero chiasma frequency). It certainly appears, from the limited material examined, as if the males of *B. tuberculatum* and *Stethophyma* spp. do have chromosomal regions with a zero chiasma frequency, and that these regions probably extend over at least 90% of the total chromosomal length.

It has repeatedly been pointed out that paracentric inversions, which seem to provide the basis for mechanisms of adaptive heterosis in many species of *Drosophila* (Dobzhansky, 1951), could hardly be expected to establish themselves and play the same role in animals with chiasmata in the males, since formation of dicentric and acentric chromatids by crossing over in inverted segments during spermatogenesis would lead to the production of many inviable zygotes.

This argument would hardly apply, however, in cases where the chiasmata are restricted to certain very short chromosomal regions, since inversions could establish themselves in other parts of the chromosomes, where chiasmata are never formed. The *Drosophila* type of adaptive heterosis does, however, depend on two essential conditions: (1) a mechanism whereby, in oogenesis, the dicentric and acentric chromatids are eliminated in the polar nuclei, and (2) the fact that in structurally homozygous females crossing-over does take place freely in the regions which show structural heterozygosity in other members of the population. There is, as yet, no direct evidence for the existence of inversions in the chromosomes of *Stethophyma* and *Bryodema*. But if conditions (1) and (2) apply in them (i.e. if there is a mechanism for the "excretion" of dicentric and acentric chromatids during oogenesis and if chiasma localization is absent or only relative in the females), then it may be that the extreme chiasma-localization of the males has an adaptive significance, since it would permit the establishment of inversions which would otherwise be eliminated by natural selection. If this is the case such species would be able to enjoy the advantages of adaptive chromosomal polymorphism and genetic recombination in the female sex, in spite of having sacrificed recombination in the males (see Carson, 1953, for a discussion of the relative advantages of recombination and adaptive polymorphism). In view of the importance of genetic recombination in adaptive evolution, it seems likely that the long chromosome regions which appear to have a zero chiasma frequency in males of *Bryodema* and *Stethophyma* either form chiasmata in the females (unlike the *Fritillaria* case where reproduction is largely vegetative) or else that certain rare genotypes in the population do have chiasmata in these regions.

The genera *Bryodema* and *Stethophyma* are not at all closely related so that their peculiar pattern of chiasma distribution must have been independently evolved. In fact, as we have seen, there are significant differences in the positions of the proximally localized chiasmata, which are formed between the centromeres and the heterochromatic blocks in *Bryodema,* while in *Stethophyma* they are on the other side of the heterochromatic segments.

The degree of chiasma localization seen in these two genera is only an extreme manifestation of a tendency which is probably present to some extent in all male grasshoppers. The great majority of the species show a combination of proximal and distal localization (the longer chromosomes showing both types, while the shorter ones show one only). Exaggeration of the distal localization with almost complete loss of the proximal chiasmata leads to the kind of distribution seen in *Paratylotropidia* (White, 1953), while the reverse development has produced the *Bryodema-Stethophyma* pattern of chiasma formation. In all such cases there is one chromosome pair with extensive heterochromatic regions which has a rather different distribution of chiasmata from that which obtains in the other members of the complement. The more extreme forms of localization are naturally always associated with very low chiasma frequencies (11–14 chiasmata per nucleus in the species we have discussed, in contrast to 13–20 in grasshoppers with less extreme localization).

The patterns of chiasma localization found in particular groups of grasshoppers are probably of considerable antiquity (there is evidence that the *Stethophyma* type is found not only in three species of that genus but also in a member of the related genus *Arcyptera*). In some instances it seems likely that the dimensions of the spindle and of the cell as a whole at the time of the first meiotic division are co-adapted to the shape of the bivalents. We have made no exact measurements on this point but it seems likely that extreme distal localization is associated with an elongated type of spindle

at first metaphase. On the other hand, the *Bryodema-Stethophyma* proximal localization requires first spermatocytes which are broad in the equatorial region, there being plenty of cytoplasm to accommodate the long horizontal arms of the longer bivalents.

The distribution of chiasmata in the structurally heterozygous Trimerotropi is a complex matter, since their pattern of localization in particular chromosome pairs depends on whether the bivalent is structually heterozygous or homozyous. But since the rearrangements are always proximal, and since they act as crossover-suppressors when heterozygous, it is obvious that all the chromosomes in which they occur must possess a strong development of distal localization. Although many of the Trimerotropi also show some degree of proximal localization as well, this does not affect the fact that ability to form a distal chiasma in most or all of the chromosomes must have been a precondition for the development of the characteristic "Trimerotropine" type of structural heterozygosity.

Systematic conclusions

Before carrying out this investigation, we expected that if any member of the Bryodemae were to be examined cytologically it would be found to show some resemblances to *Circotettix* and *Aerochoreutes,* i.e. that it would almost certainly show some metacentric chromosomes (probably including the X) and that it would possibly exhibit the same mechanism of structural heterozygosity as do the two North American genera. That *B. tuberculatum* should prove to have no metacentric chromosomes and no structural heterozygosity was hence quite unexpected. That it should possess a highly peculiar type of chiasma localization was even more so. Taken together, the cytological findings certainly suggest that this form is not nearly so closely related to the two nearctic genera as has been generally supposed.

We are not in a position to express an opinion as to how far the genera included in the Bryodemae represent a natural assemblage. It is worth noting, however, that Bey-Bienko regards *B. tuberculatum* as the nearest of the Bryodemae to *Circotettix* and *Aerochoreutes* (certain other species of *Bryodema* have the wings and elytra shortened in the female sex, which reduces their resemblance to the N. American forms). Thus it is in the form which has been studied cytologically that chromosomal similarities to the nearctic genera should be expected, rather than in the other species of *Bryodema.* The remaining genera of the Bryodemae seem to be more specialized forms, still further removed from the *Circotettix-Aerochoreutes* complex.

The close relationship of *Circotettix* and *Aerochoreutes* (together with *"Circotettix" maculatus* Scudder) to the members of section "B" of *Trimerotropis* is shown by their common possession of a large number of metacentric chromosomes and by the fact that these species either possess a mechanism of structural heterozygosity (certain chromosomes being either acrocentric or metacentric) or must be presumed to have possessed such a mechanism in the past. Evidence in favor of the same relationship is provided by the disagreement among taxonomists as to whether *suffusa* Scudder and *verruculata* (Kirby) should be assigned to *Trimerotropis* or *Circotettix.*

These American forms consequently constitute a natural assemblage for which the name "M.C. grasshoppers" (from the term metacentric) has been used (White, 1951e). The morphological diversity of this group suggests that it is an ancient one. We may accordingly discuss its relationships to section A of *Trimerotropis* (the members of which have all their chromosomes acrocentric) on the one hand and to the Bryodemae on the other. It must be emphasized that the cytological evidence clearly points to the M.C. grasshoppers as a derived and cytogenetically specialized group. Having

acquired numerous metacentric chromosomes, it is highly unlikely that they would have reversed the trend and, by a series of improbable structural rearrangements, re-converted them into acrocentrics.

Thus chromosome morphology suggests that the M.C. group could have arisen from the same stock as section A or from that of the Bryodemae, but that the reverse type of change is far less probable. However, the discovery of an extreme type of proximal chiasma localization in *Bryodema* (whereas the structural heterozygosity of the M.C. group requires distal localization) renders the origin of the M.C. group from the *Bryodema* stock highly unlikely. We are accordingly left with the conclusion that the M.C. group is closely related to the members of section A (or to some of them, at any rate, since this is a rather heterogeneous assemblage) and that any relationship to the Bryodemae is through section A or its ancestors, rather than direct. At least some of the features of resemblance, such as the thickening of the superjacent radials of the hind wing, may have been independently acquired in the Bryodemae and in the *Circotettix-Aerochoreutes* stock. Significant features of external morphology which support these conclusions are the tendency to the reduction of the wings in the females of certain Bryodemae, a tendency which does not exist in the Trimerotropines; and the development of red wing pigments in many Bryodemae. The hind wings of the Trimerotropi show yellow, greenish, or blue pigments, orange and red being unknown.

Summary

1. The grasshopper *Bryodema tuberculatum bavaricum* shows an extreme type of chiasma localization, most of the chiasmata being formed immediately adjacent to the centromeres. This kind of localization amounts to a virtual abolition of intrachromosomal recombination, the chiasmata which are formed being genetically ineffective. The distribution of the chiasmata in *Bryodema* is compared with other types of chiasma localization found in various genera of grasshoppers and some of the relationships between chiasma localization and structural heterozygosity are discussed.

2. The cytology of this species of the palaearctic genus *Bryodema* seems to preclude any very close relationship between this genus and the nearctic Trimerotropine genera *Circotettix* and *Aerochoreutes,* to which *Bryodema* shows a striking resemblance in external morphology. The Trimerotropi are consequently an autochthonous American group.

Literature Cited

(The earlier papers of Janssens, McClung, Klingstedt, and others on chiasma-localization in grasshoppers are referred to in White, 1954. Animal Cytology and Evolution, second edition.)

Bey-Bienko, G. 1930. A monograph of the genus *Bryodema* Fieb. (Orthoptera, Acrididae) and its nearest allies. Annu. Mus. Zool. Acad. Sci. U.R.S.S., **31**: 71–127.

Callan, H. G. 1942. Heterochromatin in *Triton*. Proc. Roy. Soc. Lond. B, **130**: 324–335.

Callan, H. G., and G. Montalenti. 1947. Chiasma interference in mosquitoes. J. Genet., **48**: 119–134.

Carson, H. L. 1953. The effects of inversions on crossing over in *Drosophila robusta*. Genetics, **38**: 168–186.

Darlington, C. D. 1935. The internal mechanics of the chromosomes. I, II, and III. Proc. Roy. Soc. Lond. B, **118**: 33–96.

Darlington, C. D., and L. La Cour. 1941. The genetics of embryo-sac development. Ann. Bot., N.S., **5**: 547–562.

Dobzhansky, Th. 1951. Genetics and the Origin of Species. Third edition. Columbia University Press.

Frankel, O. H. 1940. The causal sequence of meiosis. I. Chiasma formation and the order of pairing in *Fritillaria*. J. Genet., **41**: 9–34.

Maeda, T. 1939. Chiasma studies in the silkworm, *Bombyx mori*. Jap. J. Genet., **15**: 118–127.

Rehn, J. A. G. 1921. Descriptions of new and critical notes on previously known forms of North American Oedipodinae (Orthoptera; Acrididae). Second paper. Trans. Amer. Ent. Soc., **47**: 171–197.

TANAKA, Y. 1953. Genetics of the silkworm, *Bombyx mori*. Adv. Genet., **5**: 239–317.

WHITE, M. J. D. 1949. A cytological survey of wild populations of *Trimerotropis* and *Circotettix* (Orthoptera, Acrididae). I. The chromosomes of twelve species. Genetics, **34**: 537–563.

——. 1950. Cytological polymorphism in natural populations of grasshoppers. Yearb. Amer. Phil. Soc. for 1949, 183–185.

——. 1951a. A cytological survey of wild populations of *Trimerotropis* and *Circotettix* (Orthoptera, Acrididae). II. Racial differentiation in *T. sparsa*. Genetics, **36**: 31–53.

——. 1951b. Cytological polymorphism and racial differentiation in grasshopper populations. Yearb. Amer. Phil. Soc. for 1950, 158–160.

——. 1951c. Cytogenetics of Orthopteroid insects. Adv. Genet., **4**: 267–330.

——. 1951d. Evolution of cytogenetic mechanisms in animals. Chap. 16 of Genetics in the Twentieth Century. Macmillan.

——. 1951e. Structural heterozygosity in natural populations of the grasshopper *Trimerotropis sparsa*. Evolution, **5**: 376–394.

——. 1953. Multiple sex chromosome mechanisms in the grasshopper genus *Paratylotropidia*. Amer. Nat., **81**: 237–244.

——. 1954. Animal Cytology and Evolution. Second edition. Cambridge University Press.

WICKBOM, T. 1945. Cytological studies on Dipnoi, Urodela, Anura, and *Emys*. Hereditas, **31**: 241–346.

EVOLUTION AND CHROMOSOMES IN INTERGENERIC PHEASANT HYBRIDS

GUNNAR C. SANDNES

Department of Biology, Alfred University, Alfred, N. Y.

Received April 18, 1954

INTRODUCTION

Any thorough understanding of the phylogenetic relationships within a group of organisms obviously requires a knowledge of the chromosomal patterns of the species studied. Our studies on intergeneric pheasant hybrids (Danforth and Sandnes, 1939; Danforth, 1950; Sandnes, 1952) have now been supplemented by information of this kind.

A recent publication (Sandnes, 1954) pointed out the technical difficulties encountered in chromosome studies of avian material and, in addition, the handicap encountered in the case of avian hybrids when embryos or testes are used as cytological material, namely a further reduction of the small yield of specimens obtained from individual matings. A new pin-feather technique described in the same communication circumvents these difficulties, and has enabled the writer to analyze the larger chromosomes of the material under consideration.

To the degree that these observations duplicate the earlier work of Yamashina (1943, 1944) they are in complete accord and therefore confirmatory. For this reason a brief summary of the excellent but, in this country, little known work of Yamashina is here presented. Aside from their intrinsic interest these findings will be related finally to some of the evolutionary considerations which have arisen from the hybridization studies of Danforth and Sandnes mentioned above.

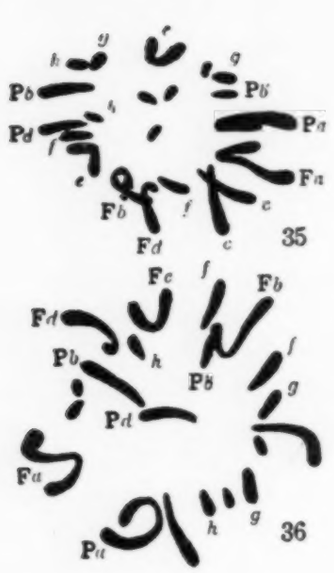
CHROMOSOMAL MORPHOLOGY

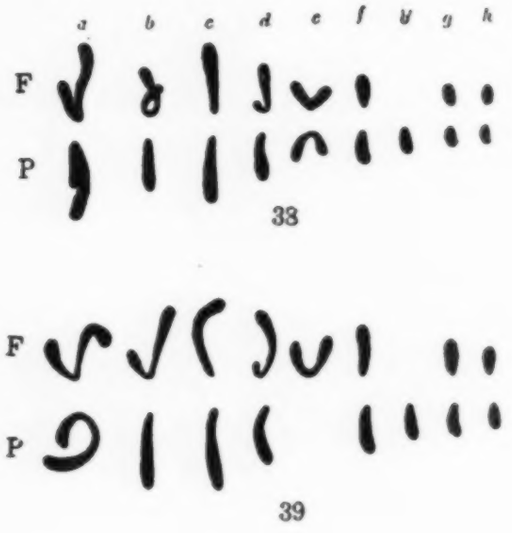
For a review of the extensive literature and a detailed report on the chromosome morphology of the domestic fowl, based on data from seventeen breeds of this species of *Gallus*, the reader is referred to Yamashina (1944). Another report by that investigator (1943) forms the basis for the discussion which follows unless otherwise indicated. Yamashina's studies with which we are concerned were based on the phasianid genera *Gallus, Phasianus, Syrmaticus* and *Chrysolophus*, and on hybrids between the first two and the last two genera. The chromosomes of *Syrmaticus* and *Chrysolophus* are reported for the first time, and the data on *Gallus* are adequate for the present purpose.

The chromosome sets of the genera *Phasianus, Syrmaticus* and *Chrysolophus* are very similar but not entirely identical. On the other hand, the chromosome morphology of *Gallus* is different from the others. Of considerable interest is the fact that neither Yamashina nor the writer could find any observable difference in the chromosome sets of the two species of *Chrysolophus* (*C. pictus* and *C. amherstiae*, Golden and Amherst pheasants respectively).

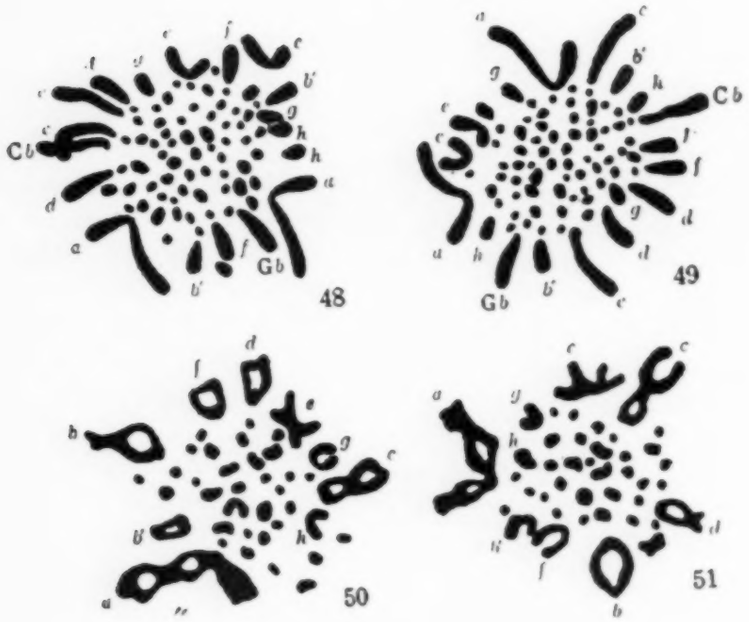
The number of chromosomes is the same in *Phasianus, Syrmaticus* and *Chrysolophus*, namely 82 in the male and 81 in the female. In *Gallus* there are reported two pairs of chromosomes less in each sex, that is, 78 in the male and 77 in the female. No W chromosome has been reported for any of these genera by recent investigators, but the possibility that it may be present submicroscopically is not excluded.

The chromosomes of *Gallus* and *Phasianus* may be compared by referring to figure 1 (Yamashina's text-figures 35–39) showing the first nine pairs of chromosomes of male and female F_1

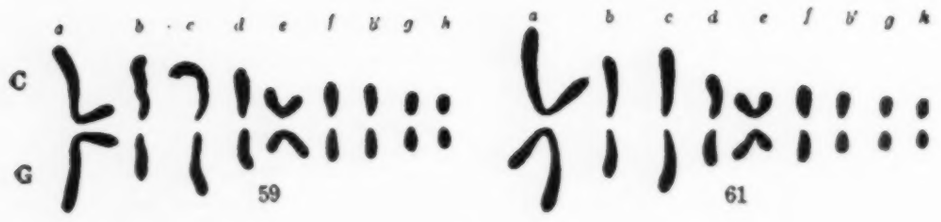

Pb
Pb
Pd
Pa
Fa
Fb
Fd
35
Fc
Fb
Fd
Pb
Pb
Pd
Fa
Pa
36


a b c d e f b' g h
F
P
38
F
P
39

1


Cb
Gb
48
Cb
Gb
49
50
51

2


a b c d e f b' g h
C
G
59
61

3

Phasianus-Gallus hybrids. It is seen that the Z chromosome is the U-shaped body, fifth in size in *Gallus* and probably fourth in *Phasianus*. In some cases in the writer's experience this chromosome seems to be third in size in *Phasianus* and *Chrysolophus*. Nevertheless the Z chromosomes of the two genera are of the same size and form.

The remaining chromosomes of *Gallus* and *Phasianus* appear identical except for those lettered b, d and b′ in Yamashina's drawings (second, fourth and seventh in the series). The b chromosome of *Phasianus* is the same length as the long arm of the b chromosome of *Gallus*. Similarly, the d chromosome of *Phasianus* is identical to the long arm of the d chromosome of *Gallus*. In Yamashina's opinion the b′ chromosome (seventh in the series) is missing in *Gallus* but represented in that genus by the short arm of the b chromosome. In a like manner he concludes that the short arm of the d chromosome of *Gallus* probably occurs as one of the smaller chromosomes (microchromosomes) in *Phasianus*. The fact that *Phasianus* has two pairs more than *Gallus* would thus be accounted for by this investigator.

The only difference in the form of the chromosomes of *Phasianus* and *Syrmaticus* that could be found was the fact that the b chromosome of *Phasianus* was slightly shorter than that of *Syrmaticus*. In a similar way it was found that the chromosomes of *Chrysolophus* differ from those of the other two genera only in that its b chromosome is in turn slightly shorter than that of *Phasianus*.

For the purpose of comparing the b chromosome lengths of these three genera, Yamashina (page 350) gives the ratios between the lengths of the b and c chromosomes in each genus. Such ratios were assumed to be reliable since the c chromosomes are "fairly equal" in each genus. The ratios given are as follows: *Syrmaticus*, 0.79; *Phasianus*, 0.77; and *Chrysolophus*, 0.68.

The chromosomes of F_1 male *Syrmaticus-Chrysolophus* hybrids were also studied by Yamashina. The chromosome sets of the two genera are normally represented as shown in figures 2 and 3. It is further seen (50 and 51 of fig. 2) that meiotic pairing is normal and that the two genera, with the minor exception of the variation in length of the b chromosomes, do not differ in any observable way. In a like manner, the writer's observations on the somatic chromosomes of *Phasianus-Chrysolophus* hybrids from repeated backcrosses to *Chrysolophus* failed to reveal any differences in the parental chromosomes.

Evolutionary Considerations

The chromosomal morphology just reviewed clearly indicates that a marked difference exists between the chromosome sets of the domestic fowl and the other three genera considered (*Phasianus, Syrmaticus* and *Chrysolophus*), that the latter differ only slightly in their chromosomal configurations, and finally that the chromosomes of the two species of *Chrysolophus* (*C. pictus* and *C. amherstiae*) are identical in appearance. The relative differentiation of the chromosomal sets coincides with the degrees of evolutionary divergence of the genera and species represented as deduced from a variety of hybridization data by Sandnes (1952).

With the exception of the very slight differences in length of one pair of chro-

Fig. 1. Macrochromosomes from somatic cells of hybrids between *Gallus* ♂ and *Phasianus* ♀. Upper two figures from male; lower from female. Designations F and P for *Gallus* and *Phasianus* respectively.

Fig. 2. Chromosomes of hybrid between *Syrmaticus* and *Chrysolophus*. Upper drawings from spermatogonial metaphases; lower from primary spermatocytes. Cb and Gb represent the b chromosomes of *Syrmaticus* and *Chrysolophus* respectively.

Fig. 3. Macrochromosomes of hybrid between *Syrmaticus* and *Chrysolophus* serially aligned. Row C from *Syrmaticus;* row G from *Chrysolophus*.

mosomes in three of the genera, it would appear that whatever chromosomal differences do exist represent no more than a separation of chromosomal arms, so the various genera must have all, or almost all, of their gene loci in common. The homologies of the chromosomal arms of other phasianid genera as well as *Gallus* and *Phasianus* were interpreted in a similar manner by Sokolow, Tiniakow and Trofimow (1936), for the three phasianid genera *Gennaeus, Meleagris* and *Numida* by Yamashina (1946), and for *Pavo,* a phasianid, and other genera from related avian families by the same investigator (1951). A more exact analysis of homology of chromosomal segments will have to await a technique for the determination of linear arrangements of chromosomal regions.

The apparently high degree of evolutionary stability of the chromosomes, including the large number of microchromosomes, is especially noteworthy. It would thus seem that the role of heterochromatin and gene position have been negligible in the speciation of the Phasianidae. A similar conclusion seems to obtain for the species of the genus *Drosophila* despite the considerable variation in chromosomal patterns found in that genus (cf. Patterson and Stone, 1952, Chapters 4 and 5).

It follows that gene mutations have been the chief hereditary factors in the speciation of phasianid forms. In this connection some reference to a paper by Danforth (1950) will be of interest. This author has demonstrated by very detailed observations that the contrasting plumage traits differentiating the genera *Phasianus* and *Chrysolophus* and the two species of *Chrysolophus* are dependent for their full expression on relatively large complexes of separately heritable units which are not of equal value so far as the main trait is concerned but consist of one, or at the most of a very few major elements that are reinforced and supported by numerous minor ones. Also very significant is the fact that the traits studied were diagnostic in the systematist's sense.

It would thus appear that the evolution of the Phasianidae has occurred mainly or entirely through the medium of one or only a few mutations in each case which must have occurred at favorable times in the history of the incipient species, and later been augmented and "fixed" in an evolutionary sense by gene modifiers. Such a process would appear to have the advantage of increasing the probability that a species may pass from one "adaptive peak" to another, since only one rather than a combination of genes would be needed for the transition. The proposed model therefore has the additional merit of being operational and simple.

The possible absence of major genes as differentiators of species in other animal groups need not of necessity preclude the possibility that their origin was brought about by such temporally tandem sequences of mutations with large phenotypical effects. The stability of a species is determined by homeostatic forces. One of these, the accumulation of modifiers, has been mentioned. A still further increase in the stability of a systematic trait could conceivably be brought about by the replacement in time of the major gene by other genes additively producing the same or a similar phenotype.

To the extent that the proposed model is saltational it is in agreement with Goldschmidt's theory of the systemic mutation (Goldschmidt, 1940), but beyond this the present writer does not venture to speculate for the time being. It is quite true that the taxonomic characters studied by Danforth are more fully expressed in the adults than in earlier stages of development; it is also true that there is a lowered fecundity (and viability) among hybrids from crosses between the various phasianid genera, but much of this may be due to a segregation among the hybrids of the numerous modifiers present in the systematic complexes just

considered (Sandnes 1952 and forthcoming papers).

Summary

The chromosomal morphology of four phasianid genera *Gallus, Phasianus, Syrmaticus* and *Chrysolophus,* including two species of the latter genus (*C. pictus* and *C. amherstiae*), is reviewed. Based on data by Yamashina (1943) with confirmation by the present writer, the results are related to the hybridization studies of Danforth and Sandnes. The findings indicate that the evolution of the Phasianidae has been saltational, and an operational mechanism which it is felt adequately relates the various facts is proposed to account for the speciation of phasianid forms.

The chromosome sets of the genera *Phasianus, Syrmaticus* and *Chrysolophus* are found to be very similar but not entirely identical. The chromosome morphology of *Gallus* is different from the others. The chromosome sets of the two species of *Chrysolophus* appear to be identical. Such differences as exist between *Gallus* and the other three genera probably represent no more than a separation of chromosomal arms, so the various genera must have all, or almost all, of their gene loci in common.

The relative differentiation of the chromosomal sets coincides with the degrees of evolutionary divergence of the genera and species represented.

This high degree of chromosomal stability suggests that gene mutations rather than chromosomal mutations have been the chief hereditary factors in the speciation of phasianid forms. This conclusion and others derived by Danforth (1950) suggest the prevailing mode of speciation among the Phasianidae. Detailed observations by the latter author have shown that the contrasting plumage traits differentiating the genera *Phasianus* and *Chrysolophus* and the two species of *Chrysolophus* are dependent for their full expression on relatively large complexes of separately heritable units. The complexes are not made up of units of equal value as far as the main trait is concerned, but consist of one, or at the most a very few major elements that are reinforced and supported by numerous minor ones. It is significant that the characteristics studied are taxonomically diagnostic.

These and other considerations suggest that the evolution of the Phasianidae has occurred mainly or entirely through the medium of one or only a few gene mutations in each case which must have occurred at favorable times in the history of the incipient species, and later been augmented and "fixed" in an evolutionary sense by gene modifiers.

Acknowledgments

A considerable part of this work was done while a graduate student in the Department of Anatomy at Stanford University. The writer takes pleasure in acknowledging his indebtedness to members of that department, and particularly to Professor C. H. Danforth for encouragement and help.

Literature Cited

Danforth, C. H. 1950. Evolution and plumage traits in pheasant hybrids. *Phasianus* × *Chrysolophus*. Evolution, **4**: 301–315.

Danforth, C. H., and Gunnar Sandnes. 1939. Behavior of genes in intergeneric crosses. J. Hered., **30**: 537–542.

Goldschmidt, R. 1940. The Material Basis of Evolution. New Haven: Yale University Press. 436 pp.

Patterson, J. T., and W. S. Stone. 1952. Evolution in the Genus *Drosophila*. New York: The Macmillan Company. 610 pp.

Sandnes, Gunnar C. 1952. Morphologic and cytogenic characteristics of hybrid Phasianidae. Ph.D. Dissertation, Stanford University: 1–146.

Sandnes, Gunnar C. 1954. A new technique for the study of avian chromosomes. Science, **119**: 508–509.

Sokolow, N. N., G. G. Tiniakow and J. E. Trofimow. 1936. On the morphology of the chromosomes in Gallinaceae. Cytologia, **7**: 466–489.

Yamashina, Yoshimaro. 1943. Studies on sterility in hybrid birds. IV. Cytological researches on hybrids in the family Phasi-

anidae. J. Fac. Sci., Hokkaido Imperial University, ser. 6, **8**: 307–386 plus 15 plates.

YAMASHIMA, YOSHIMARO. 1944. Karyotype studies in birds. I. Comparative morphology of chromosomes in seventeen races of Domestic fowl. Cytologia, **13**: 270–296.

YAMASHINA, YOSHIMARO. 1946. Chromosomes of three species of the Phasianidae (Galli). Seibutu, **1**: 42–45. (Japanese with English summary.)

YAMASHINA, YOSHIMARO. 1951. Studies on the chromosomes in twenty-five species of birds. Iden No Sógó Kenkyú (General Studies on Heredity), **2**: 27–38. (Japanese with English summary; journal title is here transliterated.)

CATEGORIES OF ADAPTATION

GARTH UNDERWOOD

Department of Zoology, University College of the West Indies, Jamaica, B.W.I.

Received June 27, 1954

INTRODUCTION

Two categories of adaptations are generally recognised. Fixed adaptations are determined in the individual by innate factors independently of its particular environmental circumstances. Facultative adaptations, sometimes called accommodations, arise in the individual in response to particular environmental circumstances. Medawar (1951) well illustrates the distinction by comparing the callosities on the hands of a gardener, "the response of an individual's tissues to irritation," with the thickening on the soles of the gardener's feet, "the response of a genetically diverse population to factors which, by promoting the survival of some variant forms rather than others, allot them different fractions of the ancestry of future generations."

Facultative adaptations correspond to Waddington's (1953b) category of "exogenous" adaptations. Those fixed adaptations which resemble facultative adaptations (as the thickening on the soles of the gardener's feet) form Waddington's "pseudoexogenous" category. The remaining fixed adaptations form Waddington's "endogenous" category.

A capacity to form callosities is a general property of terrestrial vertebrate skin. Stated in an alternative form vertebrate skin possesses a callosity forming competence. The realisation of the callosity forming competence of the palms of the gardener's hands is induced by the pressure and friction of the spade which he handles. The realisation of the callosity forming competence of the soles of the gardener's feet is due to some inductive element in the pedal morphogenetic field of the embryo. Stated thus the contrast is less striking. The capacity to form a cornea is another competence of vertebrate skin. That any external factor should directly induce realisation of this competence would have no adaptive significance; it would not, for example, be useful simply that the skin should be transparent where light fell upon it without relation to the underlying photoreceptors. The presence of an eye-cup leads to the realisation of the cornea-forming competence. This arrangement works very well in practice and ensures that the cornea develops where and only where it is useful. After a certain stage of development this competence is lost.

There is a type of adaptation which is sometimes difficult to place. A good example is dermal colour change of amphibians in response to environmental conditions. The colour of the skin is influenced by external conditions. Darkening under one set of conditions, paling under another set might be regarded as facultative adaptation. These changes are however normal short term physiological changes. The conditions to which adjustment is made vary as normally in the life of the individual as night alternates with day. The capacity for change should in this case be regarded as a fixed adaptation. Cases can be imagined in which it would be more difficult to make a clear decision.

Waddington discusses a type of facultative adaptation which is very poorly understood, exemplified by the enlargement of one kidney following the removal of the other or the thinning of the branchial epithelium of a tadpole reared in water deficient in oxygen. Perhaps this could more fruitfully be regarded as an extension of embryonic regulation.

Feet of Geckos

A rather clear example of a new adaptation which involves the development of a new competence is furnished by certain lizards. It is well known that many geckos have pads on the digits which aid in climbing. These pads consist of one or usually more scales the epidermis of which is produced into fine hairs like the pile of velvet (figured in this journal by Hecht, 1951). Mahendra (1941) has convincingly shown that these hairs aid in climbing by engaging the tiniest irregularities of the surface. To mention a few different examples: in the small geckos of the genus *Sphaerodactylus* (fig. 1, b) the pilose digital pad is formed of a single terminal scale; in *Phyllodactylus* (fig. 1, g) the pad consists of two terminal scales; *Thecadactylus* (fig. 1, f) has a straight digit bearing a large pad consisting of transverse lamellae from base to tip; *Hemidactylus* (fig. 1, e) has inflected digits, the terminal claw-bearing portion rising from the proximal pad-bearing portion.

Geckos were undoubtedly of scansorial habits before they acquired the pilose pads. The differentiation of the digital squamation undoubtedly took place under the influence of factors in the digital morphogenetic field. Moreover the squamation of the underside of the digits is nearly always differentiated from that of the upper side. Commencing with an initial roughness on the underside of the digits the pads could well have arisen by sustained selection in favour of successive small "improvements." A genetic change which produced general roughening of the scales, those on the underside of the digits included, might be favoured. However this could involve unfavourable side effects in other parts of the body. Roughness enhanced or developed under the influence of factors responsible for the differentiation of the ventral digital squamation would probably therefore be more favoured. Since differentiation of the ventral digital squamation already occurred there would probably not be need for the appearance of a new inductive factor, a new embryonic tissue response would suffice. The pads first developed involved certain particular scales.

This pad-forming competence is now obviously no longer limited to certain scales or a certain form of digit; present day geckos show a host of varieties of pads involving many different scales and in association with digits of a variety of forms. In whatever detailed manner it may have arisen in the first place the pad forming competence has become a general property of the embryonic dermis. There is some element in the digital morphogenetic field which acts as inductor. This is shown even more strikingly when we consider the genus *Lygodactylus* (fig. 1, h). The geckos of this genus have feet similar to those of *Hemidactylus* but they also have several scales on the underside of the tip of the tail modified to form a small pilose pad (Loveridge, 1947). To argue that this caudal pad appeared *de novo* without relation to the prior existence of digital pads would be unconvincing in the extreme. The evolution of the caudal pad depended on the development of a suitable inductor in the caudal morphogenetic field acting in conjunction with the already existent competence.

Callosities of Tetrapod Feet

To return to the subject of callosities let us suppose that, as one of their adaptations to life on land, the earliest tetrapods developed thickenings of the soles of their feet (as the extremities of their limbs were then becoming). This would represent a new adaptation arising in relation to the pressure and friction to which the extremities of their limbs were subjected. It would evolve as a fixed adaptive feature under the influence of natural selection. The exact details of the epidermal thickening would bear a particular relation to the particular structure and habits of the stock of organisms con-

cerned. The genetical basis of a new competence would have been synthesised; the areas of its realisation would be the soles of the feet. Such a particular epidermal thickening would be a fixed adaptive feature. The competence once established, other fixed callosities might be evolved in other parts of the body as the occasion arose (due to acquisition of new habits) by the evolution under the incidence of natural selection of new areas of induction. The capacity of the individual to form callosities facultatively in response to local pressure and friction might also arise on this foundation. It would require firstly that the callosity forming competence should not be lost during embryonic life. It would require secondly that the organism should acquire the capacity to realise the competence under the stimulus of pressure and friction—that it should, in other words, become responsive to a second inductive stimulus. The retention of an embryonic competence into adult life is not difficult to credit. We have a remarkable example of the retention of embryonic competence in the capacity of many lizards to regenerate a broken tail; sometimes the new member is scarcely distinguishable from an original. Parallels can also be found to the development of responsiveness to a second inductive stimulus. Perforation of the operculum of certain tadpoles may be effected either in response to the pressure of the growing forelimb or in the presence of the products of autolysis of the internal gills. Such a capacity for facultative adaptation as the production of callosities in response to friction is clearly a useful feature and it is not surprising that it is general in terrestrial vertebrates.

Special Callosities of the Ostrich

In the case of the ostrich discussed by Waddington (1942, 1953b) we see, with the acquisition of a new habit, the development of new fixed callosities on the underside of the body. There is in the embryo a new area of induction of callosities. This development of fixed callosities in a new part of the body is comparable to the development in *Lygodactylus* of a pad on the end of the tail.

The fact that the individual ostriches are capable of facultative formation of callosities gives the impression that there has been genetic fixation of an acquired character. The circumstances which lead in ontogeny to the formation of callosities lead separately in phylogeny to the establishment of a new field of induction in the embryo, when they persist over many generations. Waddington sketches a possible history of the early ostriches (1953b). In his stock at a stage shortly before an embryonic inductor has taken over the function of setting off the development of callosities we have ostriches with skin so responsive to external pressure and the development of callosities so canalised that a slight amount of pressure is all that is needed to set off full development of callosities. It may be pointed out that such "hypersensitive" ostriches would be liable to develop callosities, with little or no adaptive value, in all sorts of places, convenient or inconvenient, in response to the odd knocks and bruises of daily life. Waddington finally suggests that a gene mutation may occur such that some suitable part of the embryo takes over the inductive function of the external pressure. If it be necessary in the end to invoke a change of genotype to establish the suitable embryonic inductor then it may surely be invoked in the first place and thus save the ostriches from the hazards of "hypersensitization" and, presumably, from the necessity for "desensitization" after genetic fixation. Such embryonic inductors had been calling forth thickening of the soles of tetrapod feet for millions of years before the appearance of ostriches and they no doubt still thicken the soles of ostriches' feet.

Shell Form of Lymnaea

Waddington cites the example of snails of the *Lymnaea peregra* group in which forms are found with the spire of the

shell reduced (the so-called involute forms). "When they are bred in hard water, many of the races [with reduced spires] revert to normal, but in some of them the involute character is persistent and must have been gentically assimilated." It is assumed that the involute character has adaptive significance, that there is a saving of lime. There are, however, many acid waters in which involute forms have not been recorded.

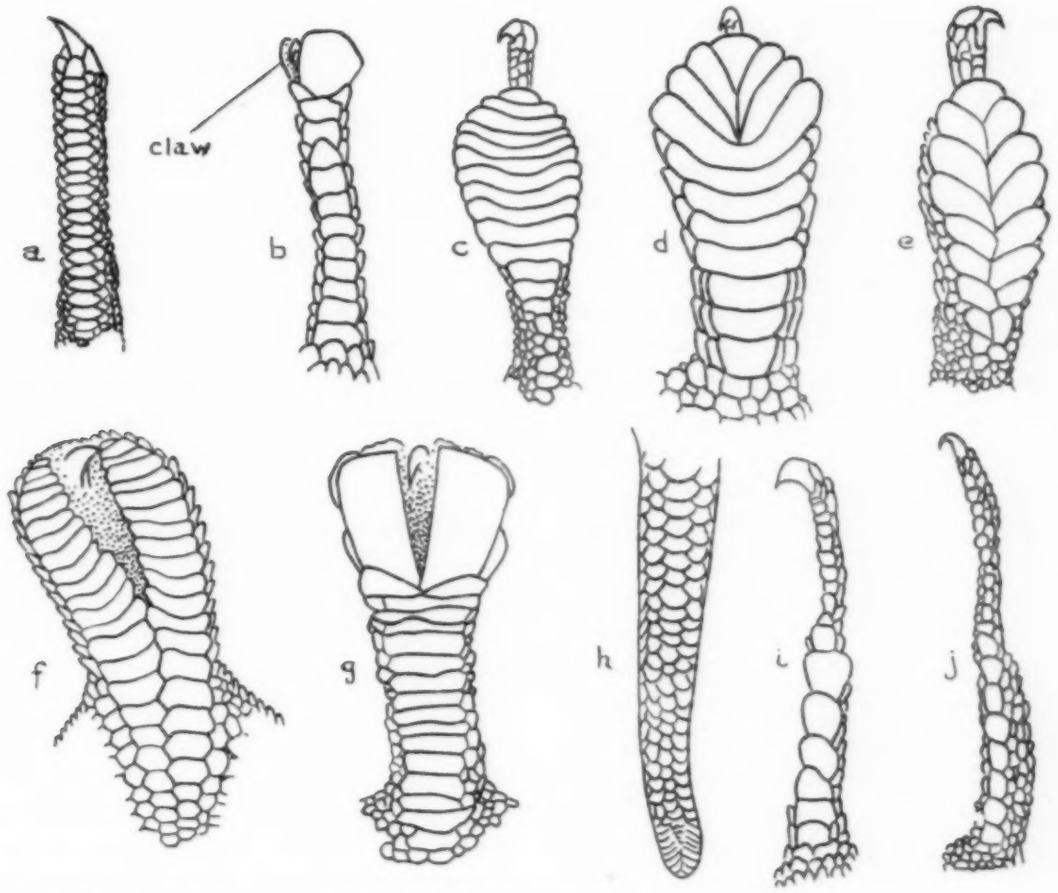
From the facts of distribution it might equally well be argued that the facultative involution has been derived from the fixed condition. There are three named subspecies in which the involute condition is fixed. They have a very broken distribution occurring in a total of five small areas in Ireland and Scotland. The phenotypically involute forms have a much wider and more continuous distribution in Ireland and Scotland. Broken distribution patterns are characteristic of old relict stocks. Continuous distribution patterns are characteristic of younger expanding stocks.

Transition from Fixed to Facultative Condition

If a species have an extensive range there may well be areas within the total range in which the "standard" form is less well adapted to the environment than in general. In such circumstances natural selection might operate in some of the special areas so to modify the genotypes as to produce individuals better adapted to the special conditions. Some of the special areas may be too small for natural selection to be effective; some may be so situated topographically that genetic exchange with the surrounding population swamps any tendency to synthesis of a special genotype. Let us consider a "special area" stock in which a fixed adaptive feature has arisen. It is not inconceivable that the appropriate phase of development of the feature should become sensitive to the conditions to which it is adaptive. This would of course involve further modification of the genotype. Such a genotype would determine an individual capable of facultative adaptation to the particular circumstances of its upbringing. On a long term view, particularly with changing topographic conditions, such a genotype might be expected to have a selective advantage. Such a genotype could do the work of the "standard" genotype plus the special genotypes synthesised in the special areas. Such a genotype would also determine individuals which would grow up well adapted to the conditions in those special areas in which special genotypes had not been synthesised. The population of individuals determined by such a genotype would also be able to keep pace with rapid changes of topography and would probably be able to colonise new areas with greater facility. In a transitional phase we might expect to find surviving in some of the older and more stable special areas populations showing the genetically fixed adaptive character, each different in detail because independently synthesised. Surrounding the pockets we might expect to find the expanding population of individuals capable of facultative adaptation, especially in the topographically complex or unstable areas. The situation in *Lymnaea peregra* might well be interpreted in this way; the stocks in which the involute condition is fixed do differ from one another in detail. The distribution of high-spired populations which are capable of facultative involution is highly relevant to the interpretation of this case; on this there appears to be no information.

Pigmentation of Human Skin

Pigmentation of human skin is an interesting adaptive feature which falls in both fixed and facultative categories. Boyd (1950) suggests that brown pigmentation of the skin was an early human characteristic later reduced in Europe. The generally heavy pigmentation of other Primates seems to confirm this. The



a) Fourth toe of *Coleonyx variegatus* (Baird). Primitively padless.
b) Fourth toe of *Sphaerodactylus parkeri* Grant. Terminal pad confined to single scale.
c) Fourth toe of *Aristelliger praesignis* (Hallowell). Pad of undivided transverse lamellae.
d) Fourth toe of *Hemiphyllodactylus typus aurantiacus* (Beddome). (Redrawn after Boulenger.) Pad of undivided and divided lamellae.
e) Fourth toe of *Hemidaetylus mabouia* (Moreau de Jonnes). Pad of divided lamellae.
f) Fourth toe of *Thecadactylus rapicauda* (Houttuyn). Pad extending length of digit, of paired transverse lamellae.
g) Fourth toe of *Phyllodactylus tuberculosus* Wiegmann. (Redrawn after Burt.) Terminal pad of two scales.
h) Underside of end of tail of *Lygodactylus picturatus*. (Redrawn after Loveridge.) Pad of paired transverse scales.
i) Fourth toe of *Gonatodes humeralis* (Guichenot). Pilose pad lost from a digit perhaps originally similar to that of *Aristelliger*. Inflection of digit and marked enlargement of proximal digital scales retained.
j) Fourth toe of *Gonatodes fuscus* (Hallowell). Further regression of proximal digital scales.

melanin forming power of vertebrates is no doubt very much older than vertebrates themselves. Throughout the vertebrate series innate factors call forth formation of melanin. The power of forming melanin is commonly retained throughout life; when an adult bird or mammal moults the new feathers or hairs are pigmented. The fair-skinned members of mankind form melanin in response to ultra-violet irradiation. Perhaps we have here the realisation in response to an external stimulus of a competence hitherto called forth only by internal genetically determined factors. It remains possible however that loss of fixed pigmentation "unmasked" a latent capacity to produce melanin under the influence of ultra-violet light. In the Himalayan (acromelanic) rabbit we have a most interesting case of realisation of melanin forming competence in response to an external stimulus, in

this case low temperature. Pigment develops only in the extremities in which the temperature is below the general body temperature. If the hair be shaved off a part of the body and the rabbit kept in cold surroundings thus cooling the hairless part, pigmented hair replaces the white hair shaved off. In a stock in which the production of melanin has been dependent on innate factors there have appeared individuals in which its production is capable of being evoked by external circumstances. These individuals appeared under experimental conditions. As it stands the response of the Himalayan rabbit to external circumstances has no adaptive value. Such a mutant may provide the sort of "raw material" from which a capacity for response of adaptive value could be synthesised on the foundation of a competence hitherto realised in response to innate factors.

Canalising Selection and Genetic Assimilation

Established in a particular niche inefficiency in other modes of life and the occupation of adjacent niches by other forms will tend to maintain the perfection of adaptation of the form concerned. Individuals in which mutant genes find deleterious expression will be subject to adverse natural selection. The elimination of such an individual will mean not merely the elimination of the gene but the elimination of an individual genotype on which, as background, the gene in question found deleterious expression. If the gene in question occur at all commonly, due to frequent mutation, the selection against the genetic backgrounds on which the gene finds deleterious expression may be more telling than selection against the gene itself.

Further, our organism established in a particular niche will not be living in perfectly uniform conditions. Some of the deviations from the optimum conditions will so influence the course of development of certain individuals as to produce adaptively inferior phenotypes. Selective elimination of the inferior phenotypes will mean elimination of a genotype which determined an individual susceptible during development to deviant environmental conditions. There will, over a long period, be sustained selection against genotypes which are liable to determine aberrant phenotypes within the commonly encountered range of environmental conditions. Such would appear to be the manner of Waddington's canalising selection.

Criticism of Waddington's choice of examples is not meant to imply criticism of the reasoning on which his theory is founded. In his experiments with *Drosophila* (1952a) the "hypothesis was tested and shown to operate as expected." Waddington (1953c) argues "that natural selection for the ability to produce an adaptive phenotype" in response to environmental circumstances "would change the genotypes in such a way as to encourage the appearance of genetically controlled variants mimicking the adaptive type." If I construe his meaning correctly then it would be more clearly expressed by stating that such selection would so change the genotypes as to increase the likelihood that some of such genetic variants as appeared would mimic the adaptive type. I do however find it difficult to believe on present evidence that Waddington's laboratory conditions are often enough approached in the field for the phenomenon of genetic assimilation to have much practical evolutionary importance.

Let us consider the *Drosophila* experiments. Exposure to a temperature of 40° C. at 17–23 hours after pupation presumably lies outside the likely experience of developing *Drosophila*. When pupae were exposed to these circumstances numbers of deviations from the normal phenotype were obtained, of which phenocopies of "crossveinless," "dumpy" and "miniature" are mentioned. That the normal development of crossveins can be buffered against temperature shock is proved by

the great reduction in the incidence of crossveinless phenocopies in the "downward" selection line. In the "upward" selection line the development of crossveins became so unstable that some crossveinless individuals appeared without temperature shock. The incidence was further increased by selection without further temperature shocks. Synthesis of such a polygenic crossveinless stock would presumably be theoretically possible without temperature shock. The temperature shock treatment makes it practically possible to achieve this by making evident those flies in which development of crossveins is initially less effectively buffered.

Waddington points out that there is "no reason to believe that the phenocopy would in nature have any adaptive value, but the point at issue is whether it would be eventually genetically assimilated if it were favoured by selection." It is difficult to see how any modification of the adult phenotype could adapt the individual to a temperature shock which it had undergone as a pupa. If it influenced the kind of eggs laid (in which case the environment would effectively operate only on females) it could adapt the next generation. It is possible that some modification of the phenotype producible under abnormal conditions could have adaptive value under normal conditions. Without initial deviation from normal conditions to reveal those individuals "leaning" in the direction of the adaptive modification natural selection would wait on an exceedingly unlikely chance congregation of genes to produce individuals showing the modification under normal conditions.

It is however entirely conceivable that a sustained deviation (in contrast to a shock deviation) from standard conditions could produce a phenotypic modification of adaptive value. If the deviant conditions persisted then canalisation would be advantageous but assimilation would be unnecessary. If the standard phenotype remained better adapted to standard conditions then assimilation would be disadvantageous if conditions fluctuated. If in fluctuating conditions intermediate degrees of modification were adaptive to intermediate environmental conditions then canalisation would be disadvantageous. Adaptive phenotypic modification in response to environmental conditions takes time. Canalisation reduces this time, but cannot abolish the gap. There will therefore remain a gap of time during which the organism is not adaptively modified, genetic assimilation can abolish this gap.

How often are conditions realised in the field in which we might expect genetic assimilation to have positive selective value? Sustained sudden changes in conditions (not brought about by human interference) must be very rare. When they do occur it is unlikely that the phenotypic modifications which they produce will have adaptive value. (This unlikelihood need not worry us too much, many individually unlikely events have happened in the course of geological time.) However, occasionally, they may have value and genetic assimilation occur.

Gradual long term changes in conditions probably take place all the time. It is difficult to see how the clean cut change of phenotype effected by canalisation can bear an adaptive relation to changes so gradual as to be imperceptible in an individual lifetime. Superimposed on long term changes are short term fluctuations, daily, seasonal and less frequent. Where development is canalised along two alternative pathways organisms born in winter (let us say) will differ sharply from those born in summer.

In the case of such organisms which live for several years it is difficult to believe that the existence of two phenotypes side by side will have adaptive value. In the case of animals with short generations like *Drosophila* there will be the intermediate seasons of spring and autumn when a mixture of summer and winter phenotypes is produced instead of intermediate phenotypes. If an organism have two generations per annum then one generation will complete its life span

under conditions differing distinctly from those experienced by the next generation. Then canalisation along two alternative developmental pathways might well be advantageous. It is interesting therefore to find that wet and dry season forms are well known in tropical butterflies. Unless however there were a one year life span and two separate breeding seasons (i.e. two separate sympatric breeding populations) genetic assimilation would be decidedly disadvantageous.

Some organisms live partly in one medium, partly in another, for example some water plants. Canalisation of development of parts such as the leaves along two pathways dependent on external circumstances is sometimes of adaptive value. If there arose from such a stock a form living in only one medium then genetic assimilation of the appropriate phenotype would be advantageous. Such phenomena, if they occur at all could account for only a minute proportion of the total of evolutionary change.

Whilst sustained sudden changes in conditions are probably very rare sharp boundaries between areas in which there is a sustained difference of ecological conditions are common. For example there may be a sharp contrast between the wet and the dry sides of mountains which stand athwart the trade winds. There is in Jamaica a sharp transition from alluvial plains country to dry scrub forest on the limestone hills. If the total range of an organism extend across such a boundary the same type is not likely to be equally well adapted to both sets of conditions. As explained above in discussing *Lymnaea* two way canalisation of development responsive to external circumstances might well be advantageous. Given fairly uniform conditions on either side of the boundary line environmental control of the phenotype would have positive value only near the boundary where population exchange between the areas is likely. The appropriate phenotype might well be genetically assimilated in either or both of the populations. The two different genetically assimilated stocks would probably differ fairly simply in genetical terms. Hybridisation would occur along the boundary. If adaptively intermediate types were produced there would be no place for them in the absence of an intermediate zone. The hybrids might also be ill regulated and genetically unbalanced. Either of these circumstances would put a premium on the development of an isolating mechanism. This would represent isolation between contiguous populations, what Mayr (1942) calls semi-geographic speciation. Such a possible situation, conceived by devious reasoning, would not be easy to recognise in the field.

It is suggested that we should distinguish as *primary fixed adaptations* those which we believe to have arisen as such, and as *secondary fixed adaptations* those which have arisen by fixation of a facultative adaptation. Similarly we may distinguish *primary facultative adaptations* which we believe to have arisen as such and *secondary facultative adaptations* which have arisen from fixed adaptations.

Modes of Adaptation

Several modes of adaptation may be distinguished. These descriptive categories grade into one another but their recognition is useful. Several of them may be illustrated by reference to the pilose dermal pads of geckos cited above.

1) *Adaptation by creation of a new feature*

This may occur at the biochemical, morphological or psychological levels. Lizards undoubtedly are primitively of terrestrial habits with simple clawed digits. We see this condition in the Eublepharid geckos (e.g. *Coleonyx*, fig. 1 a). Adaptation to scansorial habits in geckos involved the development of the remarkable pilose friction pads on certain scales on the underside of the digits. This development evidently required the synthesis of a new "aspect" of the genotype

in balanced relationship with the other already existent aspects related to established features. This must be the rarest type of adaptive change. Adaptations in this category characterise generic and higher taxonomic groups.

Some of these adaptations must arise by one of Simpson's quantum steps. Simpson (1944) discusses the manner of quantum evolution at some length. He discusses the shift of some horses from a browsing adaptive peak to a grazing adaptive peak. The browsing horses presumably lived in forest, grazing horses live in grassland. The figurative shift from browsing peak to grazing peak must have involved some actual geographical shift. Special geographical conditions may be important in such a shift. In a forest there is no grass on which to graze, there is therefore no unoccupied grazing peak. In grassland there are no trees on which to browse, there is conversely therefore no browsing peak. In special geographical circumstances we may have a forest occupied by browsing horses adjacent to savannah country in which there are no large grazing mammals. In such circumstances the savannah will offer a considerable evolutionary opportunity to the large herbivores of the forest. The greater the number of herbivores already occupying the grassland the smaller would be the evolutionary opportunity for horses and the lower the height of the by-horse-unoccupied grazing peak. The opportunity to supplement their diet with grass would be open to the horses on the forest margin. Full adaptation to grazing undoubtedly involves many factors. It might however start with a difference no greater than distinguishes related species within a genus. Let us suppose that an interspecific barrier crystallise between two populations of browsing horses which meet in a continuous forest area.

Following Gause's principle both populations will not live side by side as ecological equivalents. We would therefore expect an ecological shift if they overlap. Thus might arise from a population of browsing horses a population which, whilst preserving the general anatomical features of browsers, tended towards grass eating in their habits. In the special circumstances envisaged this would be possible because of the lack of any established grazers in the niche. A parallel to this can be cited from personal experience of Indian species of the genus *Hemidactylus* (Underwood, 1948). *Hemidactylus triedrus* (Daudin) and *H. leschenaulti* (Dumeril & Bibron) were both found abroad at night on the west side of the Deccan plateau, *triedrus* was found only on the ground in rocky grassland, *leschenaulti* was found only on trees. I do not believe that examination of preserved specimens could give any indication of the different habits. *H. triedrus* looks like a scansorial gecko. The only other species of gecko found with *triedrus* was another and much smaller species of the same genus, *H. gracilis* Blanford.

Horses once in the grass eating niche, however imperfectly adapted thereto, would with expanding population become subject to the incidence of selection pressure in a new direction. Lack of other grazers would preserve them from extermination due to interspecific competition and permit the building of the new adaptive type under the influence of intrapopulation competition. The lack of outside competition might permit rapid "rough hewing" of the new genotype without pause for adjustment of the optimum genetic balance. In these circumstances the advantage of a shift towards the new adaptive type could outweigh the disadvantage of a certain measure of genetic disequilibrium. Once the new stock makes a near approach to perfection of the new adaptive type then intrapopulational competition will again set a high premium on genetic equilibrium.

The trees of the forest offer an opportunity to geckos showing scansorial adaptive features. Such animals are probably at some disadvantage on the forest floor, the pilose pads may be clogged by mud. The one territory offers scansorial

and terrestrial adaptive peaks to nocturnal sight feeding lizards. There is some reason to believe that the shift from scansorial to terrestrial habits is more likely to occur when the scansorial peak is occupied by a number of genera.

In the Greater Antillean islands of Jamaica and Hispaniola there is but one genus of nocturnal scansorial gecko, *Aristelliger*. (*Sphaerodactylus* and *Gonatodes*, of intermediate habits with respect to daylight, are not being considered). In these islands there is no corresponding terrestrial form. There are on the South American mainland (not counting some relatives of *Sphaerodactylus*) five genera of pad-bearing geckos and three genera of padless terrestrial forms. In the comparison between the insular and mainland geckos the time factor can also be reasonably ruled out. *Aristelliger* belongs to old stock showing a relict distribution in the Antilles, nowhere overlapping a continental genus. It has no pad bearing relative surviving on the mainland, it must therefore be older than the present stock of pad-bearing geckos on the mainland. It would be interesting to know if zoogeographic evidence from other groups supports the generalisation that shift from one adaptive peak to another is more likely the more forms occupy the first peak.

2) *Adaptation by modification of existent features*

This mode of adaptation may range from a trivial level to a level at which it grades into the first category. Some geckos have digits the proximal portion of which is expanded to form a pad consisting of transverse lamellae and the distal two or three phalanges of which rise from the pad and bear a claw opposed to the free edges of the lamellae. In many of these geckos the transverse lamellae are single (e.g. *Aristelliger*, fig. 1, c). In some the distal lamellae are divided (e.g. *Hemiphyllodactylus*, fig. 1, d). In others all the lamellae are divided except the terminal (e.g. *Hemidactylus*, fig. 1, e). These seemingly trivial differences are important in the recognition of genera and probably have adaptive significance. None of the genera with all the lamellae undivided has a wide distribution. In some geckos the digit is more or less straight and a large pad extends to the tip (e.g. *Thecadactylus*, fig. 1, f), this modification has involved an increase in the area of the pad. Conversely in others the pad is restricted to the digital extremities (e.g. *Phyllodactylus*, fig. 1, g).

This must be the commonest mode of adaptation. Fixed adaptations in this category distinguish lower taxonomic categories including species and subspecies. Facultative adaptations of this kind are common and may distinguish populations and individuals. The evolution of fixed adaptations in this fashion presumably involves balanced modification of the genotype.

3) *Adaptation by extension of an existent feature to a new field*

The case of *Lygodactylus* comes in this category; a feature of the digits is extended to the underside of the tip of the tail (fig. 1, h). It should be mentioned that there is no evidence that pilose dermal pads in geckos can arise in response to friction or pressure. A specimen of *Sphaerodactylus argus dacnicolor* Barbour with one abnormally short digit shows the tip fully differentiated with claw, sheathing scales and pad. Numbers of specimens of *S. argus argus* Gosse with portions of the digits missing show no tendency to development of hairs on the scale at the tip of the stump.

It seems possible that biochemical adaptations in this category occur. An enzyme system functioning in relation to one physiological process may sometimes be capable of useful extension to other processes.

These adaptations are probably the rarest. This is not because they are "difficult" to achieve as in the case of the first category but because the circum-

stances in which they may be useful are less common. The mechanism of their evolution is discussed above.

4) *Adaptation by simplification*

Evidence is presented elsewhere that the spectacled geckos are primarily scansorial pad-bearing forms. (Underwood, in press). These spectacled geckos now include many padless terrestrial forms (28 genera out of 74). Undoubtedly there have been a number of independent reversions to terrestrial habits with loss of the digital pads. Some have evidently been derived from forms with inflected digits like *Hemidactylus* and we see stages in the reversion to a simple digital squamation (e.g. *Gonatodes,* fig. 1, i and j) whilst the inflection is retained. In others the regression is so complete that no indication of the former condition remains; just as examination of a Colubrid snake would give no indication that its ancestors possessed limbs.

Loss of features in this fashion is undoubtedly under positive selective control and is to be distinguished from degeneration. The term simplification seems more appropriate for adaptive reduction. The term degeneration may be reserved for loss of precise determination of a feature with resultant variability of no adaptive significance. The reduction in the size of the eye of a burrowing animal such as an Amphisbaenid is probably of adaptive significance, the presence or absence of lens, scleral ossicles and cartilage, the condition of the ciliary body and the degree of differentiation of the retina can scarcely have adaptive significance in an eye which no longer functions as an organ of vision.

Loss of a feature means simplification of the pattern of ontogeny and, presumably, simplification of the selective pressure on the genotype also. The loss cannot occur instantaneously for the simplification must be balanced. Balanced simplification however can surely occur more readily than balanced elaboration for simplification releases genetic variability. In the case of geckos reversion to terrestrial habits with loss of the pads is probably accomplished in a quantum step. The intermediate forms would be at a disadvantage on trees in competition with their immediate ancestors and would be at a disadvantage on soil owing to clogging of the pads.

Ecological Categories

It seems worthwhile to classify adaptations from an ecological standpoint.

1) *Subdivision of existing niche*

This involves the least profound adaptive modification. It very commonly occurs when a sibling pair of species graduates from an allopatric to a sympatric relationship. As Lack (1949) points out it is commonly found that closely related pairs of bird species are of different sizes. It does not seem probable that a niche is exactly subdivided. This would require that the part played in the biological economy by the two forms together would be the same as the one parent form originally. This category of adaptive modifications probably therefore grades into the next.

2) *Shift into a new niche*

This category of adaptive modification may involve something no more tangible than a difference of habits or it may involve creation of a new adaptive feature. At lower levels it may be occasioned by competitive relationships between closely related species. On the other hand it may form the basis for a new radiation of species and thus grade into the next category.

3) *Shift into a new adaptive zone*

Such a change must involve the creation of new features. Entry into a new zone is likely to open a number of opportunities. Diversification and occupation of new niches leads to the establishment of new generic and higher taxonomic

categories. The rank likely to be accorded to such suprageneric units varies from one phylum to another. Also relevant are degree of morphological difference and diversity and number of species.

4) *Adaptations which permit widening of the niche occupied*

These adaptations include "general improvements." I personally find it easier to believe that such an elaborate "improvement" as the system of temperature regulation of Eutherian mammals has been built up from a sequence of specific adaptive modifications, rather than to believe that there is such an evolutionary process as "general improvement."

A gecko with a very sensitive pure rod retina protected by a mobile pupil closing to a vertical slit is highly adapted to feeding by sight in dim lighting conditions. Now the majority of geckos have three lobes each on the anterior and posterior pupillary margins. These lobes so overlap when the pupil is closed as to leave four pinholes (Walls, 1942, gives an account). Such a pupil controls the amount of light entering the eye over a tremendous range and a gecko which can see to feed by moonlight can make dashes into direct sunlight to catch insects. This additional modification of what originally represented an extreme adaptation to dim lighting makes it possible for the geckos concerned to feed over a wider range of light intensities than any other lizards. Out of an extreme adaptation has arisen a "general improvement."

Perhaps the capacity to generate sufficient internal heat to maintain a body temperature above that of the surroundings represented originally in mammals an adaptation for the maintenance of nocturnal activity. (The nocturnal poikilothermous geckos are confined to warm countries.) The generation of internal heat carries with it the danger of overheating in the daytime, especially in the sunshine. The development of sweat glands making possible dissipation of excess heat allows of widening of the period of activity. The consequently more constant internal environment incidentally allows of more delicate physiological regulation.

5) *Narrowing of adaptation to a niche already occupied*

This kind of adaptation consists of an increase in specialisation. There are perhaps two categories of specialisation.

We may imagine a form confirmed in a certain mode of life in which intrapopulation competition sets a premium on closeness of correspondence between structure, function and habits. The occupation of adjacent niches by other forms would probably further discourage "deviation." Such a specialisation is positive and directional.

The specialisation of an organism closely adapted to a constant environment may represent a second category. The value of sexual reproduction in making possible the maintenance of a reservoir of genetic variability has often been stressed. Such a reservoir of genetic variability allows of adjustment to varying environmental conditions from one generation to another. If an organism live in a constant environment there ceases to be the same high premium on genetic variability. There ceases also to be the same premium on buffering of development against variations of external conditions. Environmental circumstances make simpler "demands" on the organism, the pressure of natural selection on the genotype is simplified. Thus we find that tapeworms are notoriously difficult to culture *in vitro* because they can tolerate only a very narrow range of conditions. Similarly tapeworms are regularly self fertilising, although they can cross fertilise when the opportunity offers. The specialisation of the tapeworm is only in part positive. The intolerance of variation of environmental conditions is perhaps the negative result of a process of genetic simplification.

Summary

Fixed adaptations determined by innate factors are distinguished from facultative adaptations which arise in the individual in response to particular circumstances.

Pilose dermal pads found on the feet of most geckos occur on the tip of the tail of *Lygodactylus*. Callosities found on the feet of most tetrapods occur on the underside of the body of ostriches. In both cases there has arisen a new area of induction of an already existent adaptive feature.

It is suggested that in the case of some adaptations, such as the capacity of tetrapods to form callosities, facultation has arisen from the fixed condition.

Four modes of adaptation are suggested: adaptation by (a) creation of new features, (b) modification of existing features, (c) extension of existing features to a new field, (d) simplification of existing features. These are illustrated by reference to the pilose dermal pads of geckos.

Five ecological categories of adaptive change are distinguished: (a) subdivision of an existing niche, (b) shift into a new niche, (c) shift into a new adaptive zone, (d) adaptation to a wider niche than that already occupied, (e) narrowing of adaptation to an already occupied niche, either positively under pressure of natural selection, or negatively by genetic simplification in uniform conditions.

Acknowledgment

I am indebted to Dr. W. D. Russell Hunter for information concerning *Lymnaea pereger* and for the benefit of discussion of this question.

Literature Cited

Boyd, C. C. 1950. Genetics and the Races of Man. Blackwell, Oxford.

Hecht, M. K. 1951. Natural selection in the lizard genus *Aristelliger*. Evolution, **6**: 112–124.

Lack, D. 1949. The significance of ecological isolation. Genetics, Paleontology and Evolution: 209–308. Princeton Univ. Press.

Loveridge, A. 1947. A revision of the African lizards of the family Gekkonidae. Bull. Mus. Comp. Zool., **98**: 1–469.

Mahendra, B. C. 1941. Contributions to the bionomics, anatomy, reproduction and development of the Indian house-gecko, *Hemidactylus flaviridis* Rüppel. Part II. The problem of locomotion. Proc. Indian Acad. Sci., **13**: 288–306.

Mayr, E. 1942. Systematics and the Origin of Species. Columbia Univ. Press.

Medawar, P. B. 1951. Problems of adaptation. New Biology, **11**: 10–25.

Simpson, G. G. 1944. Tempo and Mode in Evolution. Columbia Univ. Press.

——. 1953. The Baldwin effect. Evolution, **7**: 110–117.

Underwood, G. 1948. Notes on Poona reptiles. J. Bombay Nat. Hist. Soc., **47**: 627–631.

——. In press. The classification and evolution of geckos. Proc. Zool. Soc. London.

Waddington, C. H. 1942. Canalization of development and the inheritance of acquired characters. Nature, **150**: 563–565.

——. 1953a. Genetic assimilation of an acquired character. Evolution, **7**: 118–126.

——. 1953b. The evolution of adaptations. Endeavour, **12**: 134–139.

——. 1953c. The "Baldwin effect," "Genetic assimilation," and "Homeostasis." Evolution, **7**: 386–387.

Walls, G. L. 1942. The vertebrate eye and its adaptive radiation. Cranbrook Inst. Sci. Bull. 19.

HYBRIDIZATION AS AN EVOLUTIONARY STIMULUS

E. Anderson and G. L. Stebbins, Jr.

Missouri Botanical Garden and University of California, Davis

Received July 1, 1954

One of the most spectacular facets of the newer studies of evolution has been the demonstration that evolution has not proceeded by slow, even steps but that seen in the large there have been bursts of creative activity. Some of the evidence for these bursts is from paleontology; Simpson (1953) has recently assembled a wealth of data concerning them and has discussed in detail their possible causes. Paleobotanists are equally aware of such events as the great upsurge of angiosperms in the Cretaceous, and of primitive vascular plants in the Devonian period. Other evidence for evolutionary bursts comes from the existence of large clusters of related endemic species and genera in the modern fauna and flora of certain regions, particularly oceanic islands and fresh water lakes. The snails (Achatinellidae) and honey sucker birds (Drepanidae) of Hawaii are classical examples, as are also the Gammarid crustaceans of Lake Baikal, and the fishes of Lakes Tanganyika and Nyasa in Africa, and particularly of Lake Lanao in the Philippines (see Brooks, 1950 for a summary and discussion of the data). It is true that some of these examples may represent normal rates of evolution occurring in a restricted area which has been isolated for a very long time, but there can be little doubt that in the case of others evolution has been phenomenally rapid.

As Simpson (1944, 1953) has clearly stated, the cause of this rapid evolution is to be sought in the organism-environment relationship. Along with most authors, however, he has tended to emphasize the peculiar environment present during these evolutionary bursts, and has suggested that one need not postulate any unusual type of population structure as a contributing factor. Zimmermann (1948) has given a plausible account of the environmental factors operating in the case of oceanic islands; reduction of competition, frequent migration to new habitats, and populations repeatedly reduced to a very few individuals, giving a maximum opportunity for the operation of chance as well as for the rapid action of selection.

To the student of hybridization, however, another factor which may have contributed largely to these evolutionary bursts presents itself. Hybridization between populations having very different genetic systems of adaptation may lead to several different results. If the reproductive isolation between the populations is slight enough so that functional, viable and fertile individuals can result from segregation in the F_2 and later generations, then new adaptive systems, adapted to new ecological niches, may arise relatively quickly in this fashion. If, on the other hand, the populations are well isolated from each other so that the hybrids between them are largely sterile, then one of two things may happen. The hybrids may become fertile and genetically stabilized through allopolyploidy, and so become adapted to more or less exactly intermediate habitats, or they may back cross to one or both parents, and so modify the adjoining populations of the parental species through introgression. This latter phenomenon has now been abundantly documented in the higher plants, and several good examples are known in animals (see bibliographies in Anderson, 1949; Heiser, 1949; Anderson, 1953). By introgressive hybridization elements of an entirely foreign ge-

netic adaptive system can be carried over into a previously stabilized one, permitting the rapid reshuffling of varying adaptations and complex modifier systems. Natural selection is presented not with one or two new alleles but with segregating blocks of genic material belonging to entirely different adaptive systems. A simple analogy will show the comparative effectiveness of introgression.

Let us imagine an automobile industry in which new cars are produced only by copying old cars one part at a time and then putting them together on an assembly line. New models can be produced only by changing one part at a time. They cannot be produced *de novo* but must be built up from existing assembly lines. Imagine one factory producing only model 'T' Fords and another producing model 'T' Fords and also modern station wagons. It will be clear that if changes could only be brought about by using existing assembly lines these would have to proceed slowly in the factory which had only one assembly line to choose from. In the other factory, however, an ingenious mechanic, given two whole assembly lines to work with, could use different systems out of either and quickly produce a whole set of new models to suit various new needs when they arose.

Just as in the example of the two assembly lines, hybrids between the same two species could produce various different recombinations, each of which could accommodate itself to a different niche. When a big fresh water lake was formed *de novo*, hybrids between the same two species could rapidly differentiate into various new types suitable for the various new niches created in the big new lake. A technical point of much significance is that each of the various heterozygous introgressive segments brought in by hybridization would (by crossing over) be capable of producing increased variation generation after generation for periods running into whole geological eras (Anderson, 1939). The enhanced plasticity due to crossing over in introgressed segments has been shown on theoretical grounds to be present for many generations. Such studies as those of Woodson on Asclepias (1947, 1952), of Hall on Juniperus (1952) and of Dansereau on Cistus (1941) indicate that this does actually happen and that introgressive segments may persist for geological periods and produce effects of continental magnitude.

To students of introgressive hybridization it would seem like an excellent working hypothesis to suppose that when Lake Baikal was formed, and when each new island of the Hawaiian archipelago arose from the ocean, species belonging to different faunas and floras were brought together and that physical and biological barrier systems were broken down. There were increased chances for hybridization in an environment full of new ecological niches in which some new recombinations would be at selective advantages. There is a growing body of experimental data to support such an hypothesis. These data fall largely in two groups (1) Evolution under domestication, (2) Evolution in disturbed habitats.

(1) For evolution under domestication the evidence is overwhelming that by conscious and unconscious selection, man has created forms of plants and animals which are specifically distinct from their wild progenitors. This large body of evidence demonstrates that given a habitat in which novelties (or at least some of them) are at a great selective advantage, evolution may proceed very rapidly. There is presumptive evidence that many of these domesticates originated through introgression but the process began so early that getting exact experimental evidence for the history of any one of them will entail long-continued cooperative research (see, however, Mangelsdorf and Smith (1949), Alava (1952), and Nickerson (1953) for evidence that modern Zea is greatly different from the maize of five thousand

years ago and that much of this differentiation may well be the result of introgression from Tripsacum). For some ornamentals, domestication is such a recent event that critical evidence is easier to assemble. Anderson (1952) has presented in elementary detail the case of *Tradescantia virginiana*. He shows that in four hundred years by introgression from *T. ohiensis* and *T. subaspera* (unconsciously encouraged by man) it has evolved under cultivation into a variable complex quite distinct from *T. virginiana* as a genuinely wild species.

(2) Evolution in disturbed habitats. It has been repeatedly shown (Anderson, 1949; Heiser, 1949; Epling, 1947) that species which do not ordinarily produce hybrids and backcrosses may readily do so when man or any other agent disturbs the habitat. This phenomenon was referred to as "Hybridization of the Habitat" by Anderson (1948). After citing the work of several authors who have emphasized the role of man in promoting and creating habitats favorable for the perpetuation of hybrids and hybrid derivatives, he reached the following conclusion (1948, p. 6). "Does this mean that introgression as a phenomenon is limited to the areas disturbed by man and that its results are mere artifacts and not genuine natural phenomena? I think not. Though freely admitting that nearly all the introgression which has been studied experimentally (for one exception see Dansereau, 1941) is of the nature of an artifact, I believe that at particular times, and in particular places, introgression may have been a general evolutionary factor of real importance."

The great frequency of hybrid derivatives in disturbed habitats is only in part due to the breaking down of barrier systems, allowing previously isolated species to cross. It can and does occur when the barrier systems are not broken down (see for instance Heiser, 1951). Much more important is the production of new and varying ecological niches; more or less open habitats in which some of the almost infinitely various backcrosses and occasional types resulting directly from segregation in F_2 and later generations will be at a selective advantage. A particularly significant example was investigated by Anderson (unpublished) who studied *Salvia apiana* and *Salvia mellifera* in the San Gabriel mountains, confirming and extending Epling's (1947) previous studies. He found hybrid swarms not in the chaparral itself where both of these species are native but adjacent to it in cut-over live oaks amidst an abandoned olive orchard. In this greatly disturbed area, new niches were created for the hybrid progeny, which are apparently always being produced in the chaparral but at a very low frequency. In this strange new set of various habitats some of the mongrels were at a greater selective advantage and the population of the deserted olive orchard was composed of hybrids and back-crosses to the virtual exclusion of *S. apiana* and *S. mellifera*.

It has been customary to dismiss the evidence of introgression under the influence of man as relatively unimportant to general theories of evolution because nothing quite like it had previously occurred. A little reflection will show that this is not so. Man at the moment is having a catastrophic effect upon the world's faunas and floras. He is, in Carl Sauer's phrase, an ecological dominant but he is not the first organism in the world's history to achieve that position. When the first land vertebrates invaded terrestrial vegetation they must have been quite as catastrophic to the flora which had been evolved in the absence of such creatures. When the large herbivorous reptiles first appeared, and also when the first large land mammals arrived in each new portion of the world there must have been violent readjustments and the creation of new ecological niches.

The last of these (the arrival of the large land mammals) is close enough to us in geological time so that we have witnessed the very end of the process. The

vegetation of New Zealand had had no experience with mammals until the arrival of the Maori in the fourteenth century followed by Europeans in the 18th and 19th centuries. Man, pigs, horses, cattle, rats, sheep, goats, and rabbits were loosed upon a vegetation which had had no previous experience with simians or herbivores. The effect was catastrophic. Hybrid swarms were developed upon the most colossal scale known in modern times. A succession of New Zealand naturalists have occupied themselves with the problem and it has been treated monographically by Cockayne (1923) and by Allen (1937).

The extent to which disturbance of the habitat combined with reorganization of adaptive systems through hybridization could have been responsible for evolutionary bursts, "proliferation," "tachytely" or "quantum evolution" (Simpson 1953) can best be estimated by summarizing the geological and paleontological evidence concerning the time of occurrence of habitat disturbances, and comparing this with probable evolutionary changes in certain groups of organisms which were most likely initiated by hybridization. In such a survey, all three of the possible results of hybridizations—introgression, segregation of new types without backcrossing and allopolyploidy—must be considered. Reference to allopolyploids is particularly important, since hybrid derivatives of this type can easily be distinguished from their parental species by their chromosome numbers, and the time and place of hybridization can often be indicated with a high degree of probability (Stebbins, 1950, Chap. 9).

Preceding the advent of man, the most revolutionary event in the history of the northern continents was the Pleistocene glaciation and the contemporary pluvial periods of regions south of the ice sheet. This involved not only radical oscillations in climate, but also great disturbances of the soil, both in the glaciated regions and in areas to the south of them. In the latter, the extensive deposits of loess immediately south of the ice margin and the masses of alluvium carried for miles down the river valleys must have disturbed these areas almost as much as the ice sheets churned up the areas which they covered.

The activity of hybridization in developing plant populations adapted to these new habitats is amply evident from the frequency of allopolyploids in them. Specific examples are *Iris versicolor* and *Oxycoccus quadripetalus* (Stebbins, 1950); the polyploid complexes of *Salix, Betula, Vaccinium, Antennaria, Poa, Calamagrostis,* and many others can also be cited. The best example of introgression among species which have invaded the ice-free areas in post-Pleistocene time is in the complex *Acer saccharophorum* (Dansereau and Desmarais, 1947). The numerous examples cited by Anderson (1953) of hybrid and introgressant types which occupy the central Mississippi Valley between the Appalachian, Ozark, and central Texas highlands probably represent late Pleistocene or post-Pleistocene invasion of these areas which were strongly affected by outwash from the ice sheet and from the postglacial lakes. The origin of *Potentilla glandulosa* subsp. *Hanseni* in the post-Pleistocene meadows of the Sierra Nevada is discussed by Stebbins (1950, p. 279).

During the Tertiary and earlier geological periods three types of changes in the inanimate environment can be singled out which probably gave rise to disturbed habitats favorable to the establishment of hybrid derivatives. These were mountain building movements, advance and retreat of epicontinental seas, and radical changes in the earth's climate.

Some of the direct effects of mountain buildings are the rapid creation of raw, unoccupied habitats (such as lava flows, for instance), in which plants belonging to very different ecological associations may temporarily mingle and gain a chance to hybridize. In central California the canyon of the Big Sur River is a typical example of the mixing together of spe-

cies belonging to very different floras in a region of recent uplift which has a rugged, youthful topography. Here yuccas and redwoods grow within a stone's throw of each other. An example of hybridization in this area is between two species of *Hieracium; H. albiflorum,* which is typical of northern California, the Pacific Northwest, and the Rocky Mountains, and *H. argutum,* a Southern California endemic which here reaches its northern limit except for one known station in the Sierra foothills. Examples such as this could undoubtedly be multiplied by a careful study of any youthful mountain region.

The retreat of epicontinental seas in the latter part of the Pliocene period, plus faulting in the Pleistocene and recent times, has been largely responsible for the present topography of coastal California with its flat valleys and abrupt mountain ridges. One hybrid polyploid which appears to have spread as a result of these changes is the octoploid *Eriogonum fasciculatum* var. *foliolosum* (Stebbins, 1942); another is probably the tetraploid *Zauschneria californica* (Clausen, Keck, and Hiesey, 1940). A series of hybrid swarms which may have arisen in response to the same topographical changes is that of *Quercus Alvordi* (Tucker, 1952). *Delphinium gypsophilum* is a relatively well stabilized species, probably of hybrid origin, endemic to this same recently emerged area of California (Epling, 1947), and the species of *Gilia* considered by Grant (1953) to be of hybrid origin have the same general distribution. In the Old World, Dansereau (1941) has suggested that *Cistus ladaniferus* var. *petiolatus,* which occupies the recently emerged coast of North Africa, is a product of hybridization between typical *C. ladaniferus* and *C. laurifolius* both of which occur in the more ancient land mass of the Iberian Peninsula.

Among the radical changes in the earth's climate which occurred recently enough so that their effect on the vegetation can be recorded, is the advent of the Mediterranean type of climate with its wet winters and dry summers in most of California. The time of this climatic change is now fully documented by the fossil record; it took place during the middle part of the Pliocene period. It was preceded by a general decrease in precipitation, with biseasonal maxima (Axelrod, 1944, 1948).

The effects of this climatic change on the woody vegetation of the area are also well documented by the fossil record. One very probable example of a hybrid swarm exists in a fossil flora. In the Remington Hill Flora, which was laid down in the Sierra foothills at the beginning of the Pliocene, there is a great abundance of oak leaves corresponding to the modern *Q. morehus,* a hybrid between the mesophytic, deciduous *Q. Kelloggii,* and the xerophytic, evergreen *Q. Wislizenii* (Condit, 1944). That these fossil leaves were borne by hybrid trees is evidenced not only by their very unusual and characteristic shape, but also by their great variability and the fact that no similar leaves are found in any of the numerous Miocene and Pliocene floras of California. Furthermore, the Remington Hill is the only one of these fossil floras which contains the counterparts of both parental species. At present, the *Q. Kelloggii* × *Wislizenii* hybrid is frequent in the Sierra foothills, but it usually grows as single trees in company with dense stands of *Q. Wislizenii* and *Q. Kelloggii.* The populations of the parental species growing in the vicinity of the hybrids appear little or not at all different from those occurring by themselves, far from any other species of this complex. On the other hand, *Q. Wislizenii* shows considerable geographic variation, with the more northernly and more coastal variants, i.e., those adapted to increasingly mesic climates, possessing an increasingly greater resemblance to *Q. Kelloggii* in habit, leaves, buds, and fruits. This suggests that the present variation pattern in *Q. Wislizenii* is the

result chiefly of extensive introgression from *Q. Kelloggii,* which began with the hybrid swarms of Mio-Pliocene time, and has since been ordered into a regular, clinical series of variants by the selective action of the changing Pliocene and Pleistocene climates. Tucker (oral comm.) has suggested that *Q. Douglasii,* a completely unrelated oak with a similar geographical distribution, may have also originated from one or more hybrid swarms of a similar geological age. The modern variation pattern of the common chaparral species *Adenostoma fasciculatum* (Anderson, 1952) could be interpreted on the same basis, while less thorough observations by the junior author suggest that several other examples can be found in the California flora.

Conditions favorable for the origin and spread of hybrid derivatives are made not only by changes in the inanimate environment, but also by the advent and disappearance of various types of animals. Previous to man and his associated domesticates, some of these disturbances were as follows. In the Eocene and Oligocene periods, large grazing mammals made their first appearance on the earth. Their effect on the woody vegetation cannot be detected in the fossil record, and probably was not great. The herbaceous plants, however, must have been greatly affected by their inroads, and if these smaller plants had been abundantly preserved as fossils, we might be able to record a burst of evolution in them during these early Tertiary epochs. Babcock (1947, p. 132), after careful consideration of all lines of evidence, has suggested the latter part of the Oligocene as the time of origin of the genus *Crepis,* one of the larger, more specialized, and probably more recent genera of Compositae. On this basis, one might suggest that the greatest period of evolution of genera in this largest of plant families was during late Eocene and Oligocene time. The junior author, from his studies of various grass genera of temperate North America, believes that many facts about their present distribution patterns could best be explained on the assumption that they began their diversification during the Oligocene epoch. They appear to have attained much of their present diversity by the middle of the Miocene, by which time many of the now extensive polyploid complexes, such as those in *Bromus, Agropyron,* and *Elymus,* had begun to be formed. The extensive Miocene record of species belonging to the relatively advanced tribe Stipeae (Elias, 1942) would support such an assumption.

At an earlier period, namely the beginning of the Cretaceous, the world saw for a relatively short time the dominance of the largest land animals which have ever existed, the great herbivorous dinosaurs. These monsters must have consumed huge quantities of the fern and gymnosperm vegetation which prevailed at the time, and it is difficult to see how these plants, with their relatively slow growth and reproduction, could have kept up with such inroads. It is very tempting, in fact, to speculate that over grazing on the part of giant dinosaurs contributed toward the extinction of the Mesozoic gynmospermous vegetation, as well as of the larger dinosaurs themselves, during the middle of the Cretaceous period. At the same time, shallow epicontinental seas were advancing and retreating, leaving coastal plain areas open for plant colonization; other significant events during this period were the rise of modern birds and of Hymenoptera, particularly bees.

The writers venture to suggest that these four nearly or quite concurrent events—retreat of seas, overgrazing by dinosaurs, advent of a diversified avifauna which transported seeds long distances, and rise of flower pollinating bees and other insects—all contributed to the greatest revolution in vegetation which the world has even seen; the replacement of gymnosperms by the predominant angiosperm flora of the upper part of the Cretaceous period. One should note that all of these conditions would favor hy-

bridization and the spread of hybrid derivatives, by giving unusual opportunities for previously separated types to be brought together by wide seed dispersal, by permitting cross pollination between types previously isolated from each other, and by opening up new areas for colonization by the hybrid derivatives. The suggestion has been made elsewhere (Stebbins, 1950, p. 363) that differentation of genera and sub-families among primitive angiosperms took place partly via allopolyploidy; the time of origin of this polyploidy may well have been during the Cretaceous period. Evidence of introgression at so remote a time is probably impossible to obtain; by an analogy we should assume that in the past as now, conditions favorable for allopolyploidy also promoted introgression.

Going still further into the past, let us speculate on the events which must have taken place at the time when vascular plants and vertebrates first spread over the land. The principal geological period involved is the Devonian. At the beginning of this period comes the first extensive fossil record of vascular plants, all belonging to the primitive order Psilophytales. By the end of the Devonian, forms recognizable as club mosses (Lycopsida), ferns (primitive Filicales), and seed plants (Pteridospermae) were already widespread. We shall, of course, never know what chromosome numbers existed in these extinct groups of primitive vascular plants. But their nearest living descendants are nearly all very high polyploids, as has now been most elegantly demonstrated by Manton (1950, 1953). She has suggested that the living Psilotales, which have gametic numbers of about 52, 104, and over 200, "are the end-products of very ancient polyploid series which date back to simple beginnings. . . ." The relationship between the modern Psilotales and the Devonian Psilophytales is not clear, but to the present authors they appear to resemble each other nearly enough so that they could belong to the same complex network of allopolyploids, which developed its greatest diversity in the Devonian period. In the genus *Ophioglossum,* generally regarded as one of the three most primitive genera of true ferns, we have the highest chromosome numbers known to the plant kingdom, namely n = ca. 256 in the northern *O. vulgatum* and n = ca. 370 in the tropical *O. pendulum*. These ferns are not preserved in the fossil record because of their soft texture, but their origin during the Devonian period is a fair inference. There is very good reason to believe, therefore, that the great proliferation of genera and families of vascular plants during this earliest period of their dominance was accompanied by allopolyploidy just as it has been in the more recent periods of very active evolution. Where allopolyploidy was widespread, we can also suspect abundant introgression.

The reader may well ask at this point whether any of this evidence contributes to the central theme of the present discussion, namely the hypothesis that these extensive hybridizations, both ancient and relatively modern, gave rise to really new types, which formed the beginnings of families, orders, and classes having different adaptive complexes from any plants previously existing. It is undoubtedly true that the results of introgression and allopolyploidy are chiefly the blurring of previously sharp distinctions between separate evolutionary lines, and the multiplication of variants on adaptive types which were already established during previous cycles of evolution. Nevertheless, the fact must not be overlooked that conditions favorable for introgression and allopolyploidy, namely the existence of widely different and freely recombining genotypes in a variety of new habitats, also favor the establishment and spread of new variants. Establishment of new adaptive systems is under any circumstances a relatively rare event; in any group of organisms we have hundreds of species and subspecies which are variants of old adaptive types to one which repre-

sents a really new departure. Hence we cannot expect to recognize introgressive or polyploid complexes which have given rise to such new types until we have carefully analyzed hundreds of those which have not. Furthermore, our methods of recognizing these complexes almost preclude the chance of identifying the new types which have arisen from them. We make the assumption that hybrid derivatives, whether introgressants or allopolyploids, have characteristics which can all be explained on the basis of intermediacy between or recombination of the characteristics of the putative parents, and then devise methods of verifying this assumption. The new types, falling outside of this assumption, would be rejected by our methods.

The junior author can suggest two examples known to him of new and distinctive morphological characteristics which may have arisen in recent hybrid derivatives. One of these is the presence in *Ceanothus Jepsonii,* a species narrowly endemic to the serpentine areas of northern California, of flowers with six and seven sepals, petals, and anthers (Nobs, 1951). This characteristic is not known anywhere else in the family Rhamnaceae or even in the entire order Rhamnales, an order which almost unquestionably dates back to the Cretaceous period. Mason (1942) has given strong evidence for the recent origin of *Ceanothus Jepsonii.* It inhabits an environment which is certainly recent, since the mountains on which it occurs were covered by a thick layer of volcanic rocks even as late as the end of the Pliocene epoch, and the serpentine formations to which it is endemic were not exposed until after the faulting which occurred at the beginning of the Pleistocene (Mason, 1942). It belongs to a complex of closely related species and subspecies, among which hybridization is still very actively taking place (Nobs, 1951). In characteristics other than sepal and petal number, it is intermediate between various ones of its relatives rather than an extreme type. Hence there is a good reason to suspect that *Ceanothus Jepsonii* represents a species of relatively recent (i.e. Pleistocene) hybrid origin which has evolved a morphological characteristic previously unknown in its family, and in fact one which is relatively uncommon in the entire subclass of dicotyledons.

The other example is in the grass species *Sitanion jubatum.* This species is distinguished by possessing glumes which are divided into a varying number of linear segments, a characteristic not found elsewhere in the tribe Hordeae, and one which is the basis of a distinctive mechanism for seed dispersal (Stebbins, 1950, p. 141). *Sitanion jubatum* is endemic to Pacific North America, being most abundant in the coast ranges and foothills of central California. Its nearest relative is *S. hystrix,* a species found in the montane areas of the same region, and extending far eastward and southeastward. The two species are distinguished only by the degree of division of the glumes, and in fact appear to grade into each other. Field observations suggest that they actually consist of a large swarm of genetically isolated microspecies, such as has been demonstrated experimentally to exist in the related *Elymus glaucus* (Snyder, 1950).

Cytogenetically, both species of *Sitanion* are allotetraploids (Stebbins, Valencia, and Valencia, 1946). Extensive chromosome counts from various parts of the ranges of both species plus still more numerous measurements of sizes of pollen and stomata have failed to reveal any form of *Sitanion* which could be diploid. Furthermore, the chromosomes of both species are strongly homologous with those of *Elymus glaucus,* as evidenced by complete pairing in the F_1 hybrid. All of this evidence suggests that *S. jubatum* did not have any diploid ancestors which possessed its distinctive glumes, but has evolved out of a complex of allopolyploids which has existed in western North America for a long

time, probably since the middle of the Tertiary period.

The forms of *S. jubatum* which have the most extreme division of the glumes occupy habitats which are recent, and which in some ways are intermediate between the most extreme habitats occupied by *Sitanion* and those characteristic of *Elymus glaucus*. They are known from the shore of San Francisco Bay, in northeastern Marin County, from the eastern edge of the Sacramento Valley north and east of Sacramento and from the Sierra foothills in Mariposa county. In growth habit, these races of *S. jubatum* could be regarded as intermediate between the most extreme xerophytes found in *Sitanion* on the one hand, and *E. glaucus* on the other.

Experimental evidence (Stebbins, unpublished) has now indicated that the complex of microspecies within the taxonomic species *Elymus glaucus* originated partly if not entirely through introgression. The probability is strong that *Sitanion* consists of a similar swarm of microspecies which originated also by introgression. The extensive subdivision of the glumes in some of these microspecies, therefore, may well have originated through the establishment of new mutations, or of new types of gene interaction, in genotypes produced by hybridization and introgression between morphologically very different and genetically well isolated species.

When all of this evidence has been considered, the writers can hardly escape the conclusion that hybridization in disturbed habitats has produced the conditions under which the more familiar processes of evolution, mutation, selection, and the origin of reproductive isolation barriers, have been able to proceed at maximum rates. Far from being insignificant because much of it is in habitats greatly disturbed by man, the recent rapid evolution of weeds and semi-weeds is an indication of what must have happened again and again in geological history whenever any species or group of species became so ecologically dominant as greatly to upset the habitats of their own times.

Summary

(1) It has been established by recent work in Palaeontology and Systematics that evolution has not proceeded at a slow even rate. There have instead been bursts of evolutionary activity as for example when large fresh water lakes (Baikal, Tanganyika, and Lanao) were created *de novo*.

(2) Recent studies of introgression (hybridization and subsequent back-crossing) have demonstrated that under the influence of man evolution has been greatly accelerated. There has been a rapid evolution of plants and animals under domestication and an almost equally rapid evolution of weed species and strains in greatly disturbed habitats.

(3) The rapidity of evolution in these bursts of creative evolution may well have been due to hybridization. At such times diverse faunas and floras were brought together in the presence of new or greatly disturbed habitats where some hybrid derivates would have been at a selective advantage. Far from being without bearing on general theories of evolution, the repeated demonstrations of accelerated introgression in disturbed habitats are of tremendous significance, showing how much more rapidly evolution can proceed under the impact of a new ecological dominant (in this case, Man). Such an agent may bring diverse faunas and floras into contact. Even more important is the creation of various new, more or less open habitats in which novel deviates of partially hybrid ancestry are at a selective advantage. The enhanced evolution which we see in our own gardens, dooryards, dumps and roadsides may well be typical of what happened during the rise of previous ecological dominants. The first vertebrates to enter isolated continents or islands, the first great herbivorous reptiles, the first herbiv-

orous mammals must have created similar havoc upon the biotae of their own times. Introgression must have played the same predominant role in these disturbed habitats as it does today under the impact of man. These arguments are supported by a homely analogy (page 379) and by various kinds of experimental and taxonomic data.

Literature Cited

Alava, Reino O. 1952. Spikelet variation in *Zea Mays L.* Ann. Mo. Bot. Gar., **39**: 65–96.

Allan, H. H. 1937. Wild species-hybrids in the phanerogams. Bot. Rev., **3**: 593.

Anderson, E. 1939. Recombination in species crosses. Genetics, **24**: 688.

——. 1948. Hybridization of the habitat. Evolution, **2**: 1–9.

——. 1949. Introgressive Hybridization. Wiley & Sons, New York, 109 pp.

——. 1952. The ecology of introgression in Adenostoma. Nat. Acad. Sci.: Abstracts of papers presented at the autumn meeting, Nov. 10–12, 1952 (Sci., **116**: 515–516).

——. 1952. Plants, Man and Life. Little, Brown & Co., Boston, 245 pp.

——. 1953. Introgressive hybridization. Biol. Rev., **28**: 280–307.

Axelrod, D. I. 1944. The Pliocene sequence in central California. Carnegie Inst. Wash. Publ., 553: 207–224.

——. 1948. Climate and evolution in western North America during Middle Pliocene time. Evolution, **2**: 127–144.

Babcock, E. B. 1947. The genus *Crepis*. Part I. The taxonomy, phylogeny, distribution and evolution of *Crepis*. Univ. Calif. Publ. Bot., **21**: 1–198.

Brooks, J. L. 1950. Speciation in ancient lakes. Quart. Rev. Biol., **25**: 131–176.

Clausen, J., D. D. Keck and W. Hiesey. 1940. Experimental studies on the nature of species. I. Effect of varied environment on western North American plants. Carnegie Inst. Wash. Publ., 520, vii, 452 pp., figs. 1–155.

Cockayne, L. 1923. Hybridism in the New Zealand flora. New Phytol., **22**: 105–127.

Condit, C. 1944. The Remington Hill flora. Carnegie Inst. Wash. Publ., 553: 21–55.

Dansereau, P. 1941. Etudes sur les hybrides de Cistes. VI. Introgression dans la section Ladanium. Can. Jour. Research, **19**: 59–67.

—— and Y. Desmarais. 1947. Introgression in sugar maples. II. Amer. Midl. Nat., **37**: 146–161.

Elias, M. K. 1942. Tertiary prairie grasses and other herbs from the high plains. Spec. Papers Geol. Soc. Amer., 41: 176 pp.

Epling, C. 1947. Actual and potential gene flow in natural populations. Am. Nat., **81**: 81–113.

——. 1947. Natural hybridization of *Salvia apiana* and *S. mellifera*. Evolution, **1**: 69–78.

Grant, V. 1953. The role of hybridization in the evolution of the leafy-stemmed *Gilias*. Evolution, **7**: 51–64.

Hall, M. T. 1952. Variation and hybridization in *Juniperus*. Ann. Mo. Bot. Gard., **39**: 1–64.

Heiser, C. B., Jr. 1949. Natural hybridization with particular reference to introgression. Bot. Rev., **15**: 645–687.

——. 1951. A comparison of the flora as a whole and the weed flora of Indiana as to polyploidy and growth habits. Indiana Acad. Sci., Proc., **59**: 64–70.

Mangelsdorf, P. C., and C. E. Smith, Jr. 1949. New archeological evidence on evolution in maize. Bot. Mus. Leaflets, Harvard Univer., **13**: 213–247.

Manton, I. 1950. Problems of Cytology and Evolution in the Pteridophyta. 316 pp., Cambridge University Press.

——. 1953. The cytological evolution of the fern flora of Ceylon. Soc. Exp. Biol., Symp., **7**: Evolution, 174–185.

Mason, H. L. 1942. Distributional history and fossil record of *Ceanothus*. pp. 281–303 in Van Rensselaer, M., and H. E. McMinn. *Ceanothus*, publ. by Santa Barbara Bot. Gard., Santa Barbara.

Nickerson, N. H. 1953. Variation in cob morphology among certain archaeological and ethnological races of maize. Ann. Mo. Bot. Gard., **40**: 79–111.

Nobs, M. 1951. Ph.D. Thesis, Univ. California, Library.

Sauer, C. O. 1952. Agricultural origins and dispersals. Am. Geogr. Soc., Bowman memorial lectures Ser. II, v. 110 pp., 4 pls. New York.

Simpson, G. G. 1944. Tempo and Mode in Evolution. xiii, 237 pp., New York.

——. 1953. The Major Features of Evolution. Columbia University Press, New York, 434 pp.

Snyder, L. A. 1950. Morphological variability and hybrid development in *Elymus glaucus*. Amer. Jour. Bot., **37**: 628–636.

Stebbins, G. L., Jr. 1942. Polyploid complexes in relation to ecology and the history of floras. Am. Nat., **76**: 36–45, figs. 1–2.

——. 1950. Variation and Evolution in Plants. Columbia University Press, New York, 643 pp.

——, J. I. VALENCIA AND R. M. VALENCIA. 1946. Artificial and natural hybrids in the Gramineae, tribe Hordeae I. *Elymus, Sitanion* and *Agropyron*. Am. Jour. Bot., **33**: 338–351.

TUCKER, M. 1952. Evolution of the California oak *Quercus alvordiana*. Evolution, **6**: 162–180.

WOODSON, R. E., JR. 1947. Some dynamics of leaf variation in *Asclepias tuberosa*. Ann. Mo. Bot. Gard., **34**: 353–432.

——. 1952. A biometric analysis of natural selection in *Asclepias tuberosa*. Nat. Acad. Sci.: Abstracts of papers presented at the autumn meeting, Nov. 10–12, 1952 (Sci., **116**: 531).

ZIMMERMAN, E. C. 1948. Insects of Hawaii. Vol. I. Introduction. University of Hawaii Press, Honolulu, 206 pp.

THE FORAMEN OVALE

TILLY EDINGER[1] AND DAVID B. KITTS

Museum of Comparative Zoölogy at Harvard College, Cambridge, Massachusetts, and School of Geology, University of Oklahoma, Norman, Oklahoma

Received July 2, 1954

INTRODUCTION

We recently have studied the cranial nerve foramina in American specimens of the oldest of the Equidae, the early Eocene *Hyracotherium* (eohippus). Our description will not be published in its present form since, during the summer of 1953, a party from the American Museum of Natural History excavated the first undistorted eohippus skulls ever found in America. In the crushed crania we had at hand we have, however, observed one detail which we found to be of general significance.

The mandibular branch of the trigeminal nerve (V^3) appears to have been variable in its relations to the wing of the sphenoid bone (ala temporalis sphenoidei, alisphenoid). The *Hyracotherium* skulls A.M.N.H.[2] 4832 and 4831 on their right sides contain the alisphenoid relatively well preserved. In the first specimen we could not detect any trace of perforation in the wing of the sphenoid. In this individual, consequently, the mandibular nerve must have passed outward posterior to that bone as in *Equus* (fig. 1). It must have shared with the internal carotid and middle meningeal arteries the anterior section of the foramen lacerum (variously termed f. lac. anterius or medium). In the second specimen, a slit extends forward from the foramen lacerum into the sphenoid wing. Here, apparently, passage of the mandibular nerve was anterior to the foramen lacerum but without osseous separation from that basicranial gap. A third specimen (Y.P.M.-V.P. 11694) is undistorted. It was labelled Eohippus by O. C. Marsh, but it cannot be definitely determined because no teeth are preserved. Since this cranium was described (as eohippus, Edinger, 1948), loss of a small piece of bone has revealed a foramen lying anterior to the foramen lacerum from which it is separated by a thin, transverse, perpendicular bony septum. This individual thus possessed a foramen ovale. Its mandibular nerve emerged here, that is, through the wing of the sphenoid as in the majority of mammals, including monotremes and marsupials.

These three different conditions are noteworthy because their presence in three crania which possibly belong to one genus disagrees with current opinion on cranial foramina in the class Mammalia. "They are very useful in classification, since the presence or absence of certain foramina differentiates orders very clearly" (Adams and Eddy, 1943, p. 172). The foramen ovale is supposed to be one of these foramina. While of other cranial foramina the literature records even intraspecific variability in their being separate, or confluent either on the inside or the outside of the cranium or both, "foramen ovale . . . separate"[3] is listed among the characteristics of Artiodactyla in the standard work on extant and extinct mammals (Weber & Abel, 1928, p. 521). In Perissodactyla, "The tympano-

[1] This paper is one of a series aided by a grant, to the senior author, from the Penrose Fund of the American Philosophical Society.

[2] We use the following abbreviations: A.M.N.H. (American Museum of Natural History, New York, N. Y.); M.C.Z. (Museum of Comparative Zoology at Harvard College, Cambridge, Mass.); P.U. (Princeton University Geological Museum); U.S.N.M. (United States National Museum, Washington, D. C.); Y.P.M. (Peabody Museum, Yale University, New Haven, Conn.).

[3] Foreign language quotations are translated.

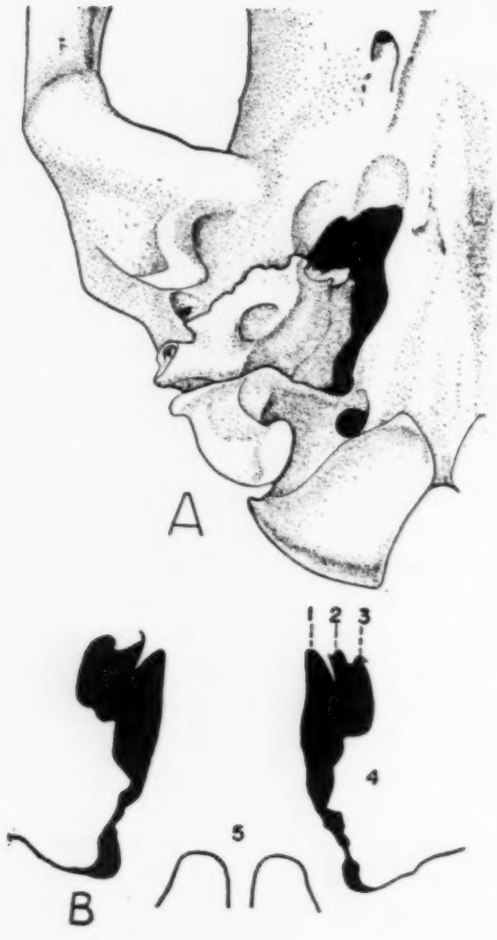


FIG. 1. Recent perissodactyl, *Equus caballus*. *A:* Right side of cranium, ventral view (M.C.Z. Mamm. Dept. 1713). Black, from front to back: Foramen alare parvum (of alar canal), f. lacerum, f. hypoglossi. × ⅔. *B:* Right and left foramen lacerum of Sisson's specimen; *1:* Incisura carotica, *2:* i. ovalis, *3:* i. spinosa, *4:* bulla tympanica, *5:* basilar part of occipital bone.

periotic is . . . separated from the basioccipital and sphenoid by a wide gap which corresponds to the foramen lacerum, f. jugulare, f. caroticum, f. ovale, and f. spinosum, and thus serves the passage of . . . the third branch of the trigeminal nerve," etc. (*ibid.*, p. 638).

Indeed there appears to be a striking difference between artiodactyls and perissodactyls with regard to the cranial passage of V^3 if one chooses for comparison skulls of, e.g., deer and horse. The anterior part of the foramen lacerum is comparatively narrow and is adjoined by a foramen ovale in *Odocoileus* (fig. 2 B). It is wide and includes the mandibular nerve in *Equus*.

If presence and absence of foramen ovale really constituted differences distinguishing mammalian orders, these characters might provide the highly desirable means for an at least ordinal determination of fossil skull fragments lacking teeth. Also, it would signify that only the first of our three early Eocene specimens is perissodactyl.

Besides such high taxonomic value, evolutionary significance too is attributed to the presence of a mandibular nerve foramen separate from the lacerum. "Individualization of cranial foramina is a sign of progressive evolution" (Hecker & Grünwald, 1926b, p. 361). Under that concept, our three specimens would form an evolutionary series with regard to the mandibular nerve exit. The third, by possessing a distinct foramen ovale, would appear to have attained a higher level of evolution than the second and, particularly, the first.

Briefly, our few special data are at variance with current opinion generally adopted at least in neontology. We found other cases inconsistent with that concept described in the literature, particularly of paleontology. These published data, however, are few and scattered incidental remarks on the foramen ovale in this or that skull. They did not carry sufficient weight for revision of a long-standing doctrine. We, therefore, felt obliged to undertake a general survey of the foramen ovale area. In the course of our study the *Hyracotherium* and ?eohippus specimens became incidental and the generic identity of the latter unimportant. Many other skulls of fossil and also of recent mammals convincingly show that current opinion about the significance of the foramen ovale must be rejected. The specimens we can cite as constituting a record of mandibular nerve exits in extinct ungulates may appear small in number; but only they, of course, are documents of evolution. The usual

handicap of paleontology compared with neontology, the scarcity of available specimens and of relevant literature data, was particularly great in our study of a small detail owing to circumstances of different sorts.

1) The temporal wing of the sphenoid bone, which either encloses or lacks a foramen ovale, is an area predestined to break in the process of skull fossilization. It is a relatively thin plate stretched transversely between the massive basilar part of the cranium and that part of the temporal bone which is fortified for articulation with the lower jaw. It has, in consequence, been destroyed in many fossil specimens, and when present is usually distorted.

2) Preparators have rarely cleaned the foramen lacerum area of the overlying and, particularly, the filling matrix. Even when preservation is reasonably good, matrix usually left *in situ* blurs details of foramen margins and directions. For the identification of an opening in a fossil skull, position is sometimes not sufficient; the direction of the cranial perforation is then decisive: below are quoted cases in which we determined as alar canal and foramen rotundum, respectively, openings regarded by earlier authors as foramen ovale. A great deal of specimen preparation would be a preliminary to a study based on more material than was available to us.

3) While zoologists decided that the foramen ovale is a feature of great taxonomic importance in ungulates and of evolutionary significance in mammals as a whole, paleontologists paid little attention to that small detail. Many descriptions of fossil mammal skulls do not even mention cranial foramina. This is reflected in the published figures. Artists, we found repeatedly, were allowed to embellish or otherwise misrepresent the area we studied in the figured specimens.

Artiodactyla

The artiodactyls do not conform with the textbook postulation even in their Recent representatives. A separate cranial passage for the mandibular nerve is not present in all members of this vast and varied order.

Examining the skulls of Recent Artiodactyla in the M.C.Z. Department of Mammals, we saw no deviations from the supposedly artiodactyl characteristic in the suborder [4] Ruminantia. The extinct ruminants, too, were apparently all provided with an individual foramen ovale.

In the suborder Tylopoda, however, the two surviving genera—members of the same subfamily, Camelinae—differ considerably in the morphology of the foramen lacerum area. Three species are represented in the collection of the Mammal Department of the Museum of Comparative Zoölogy. All five specimens of

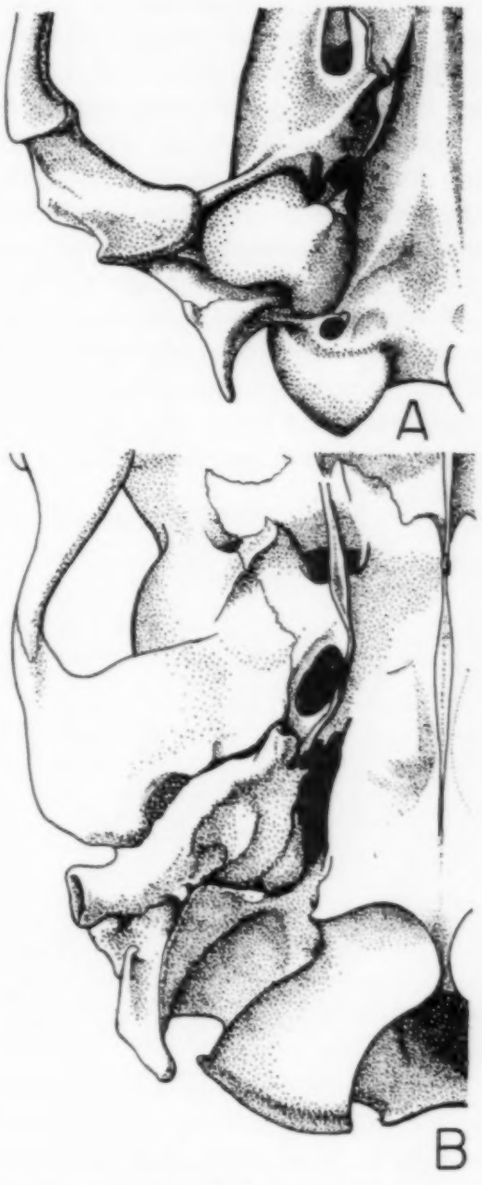


Fig. 2. Recent artiodactyls. Right side of crania. *A: Tayassu torvus*, ventro-posterior view (M.C.Z. Mamm. Dept. 8291). × ¾. *B: Odocoileus hemionus*, ventral view (M.C.Z. Mamm. Dept. 29879). Black: Foramen orbitorotundum, f. ovale, f. lacerum, f. hypoglossi. × ⅚.

[4] The classification of Simpson, 1945 is followed throughout this paper.

Camelus bactrianus have a foramen ovale well separated from the lacerum, as in the ruminants. These camels have retained the condition present in the Lower Pliocene cameline, *Procamelus* (e.g., M.C.Z. 4447), and in the probable ancestor of the Camelinae, the Middle Oligocene *Poëbrotherium* (e.g., M.C.Z. 16387 and 17684). But there is no such perforation of the alisphenoid in 7 skulls at hand of *Lama huanachus* and in the 5 skulls of *Lama vicugna*. All, however, have a delicate osseous separation within the foramen lacerum of a lateral section which lies in a sagittal plane corresponding to but more posterior than the foramen ovale of the camel. This superficial division of the foramen lacerum consists of a thin longitudinal spine extending backward from the posterior margin of the alisphenoid. The length of this spine is extremely variable. In some vicugna skulls a complete longitudinal bridge is formed, the spine being met by a shorter forward process from the auditory bulla, as in some pigs.

In the suborder Suiformes all Eocene and Oligocene representatives apparently had the foramen ovale. It is seen, for example, in the most ancient infraorder, Palaeodonta, in Pearson's (1927) figures of *Mixtotherium* (fig. 33) and *Cebochoerus* (fig. 23); also, in early representatives of the next-oldest infraorder, Ancodonta; *Brachyodus* (fig. 31), *Haplobunodon* (fig. 39), and *Diplobune* (fig. 43). In the ancodont family Caenotheriidae, which became extinct early in the Miocene, numerous late Oligocene specimens with foramen ovale are known (basal view figures of 6 specimens in Hürzeler, 1936).

The foramen is, however, lacking in later forms. Its loss has been traced in the history of another ancodont family, the Anthracotheriidae; "The basicranial foramina are quite separate in the primitive forms, but in some of the advanced genera, such as *Merycopotamus*" (Middle Pliocene to Lower Pleistocene)," they are coalesced around the bulla" (Colbert, 1935a, p. 12). In the surviving family of Ancodonta, the Hippopotamidae, the broad gap between auditory bulla and sphenoid bone serves as foramen lacerum + ovale in all three known genera: the middle Pliocene to Lower Pleistocene *Hexaprotodon* (Colbert, 1935b, p. 285) and the extant *Hippopotamus* and *Choeropsis*.

In the infraorder Suina, van Kampen described the extant Suidae as having "the foramen ovale not closed by encirculating bone, but only an incisure in the posterior margin of the alisphenoid, and usually separated but incompletely from the foramen lacerum anterius by a small process of the latter bone" (1905, p. 538); but Sisson says of *Sus:* "The foramen ovale is absent, being included in the foramen lacerum anterius" (1938, p. 171). The contradiction is in terms. It results from the widespread development, in the Suidae, of the backward alisphenoid spine (fig. 2 A) we observed in the llama (and in a rhinoceros, see below). This spine can so divide the foramen lacerum as to produce the impression that the prootic gap consists of two foramina. Actually, each of these is only a segment of the lacerum, set off only superficially, never in depth. Neither is a homologue of the more anterior foramen piercing the alisphenoid in the early ancestors of *Sus*. The lateral one, whether notch or hole, is analogous to the foramen ovale. Indeed, a dissection of an adult male domestic pig revealed that this lateral notch contained only the mandibular nerve root.

In detail, the conditions in the Suidae are as follows. In all the dozens of skulls we studied, there is some development of a spicule extending backward from the alisphenoid into the foramen lacerum. But the figures in the literature giving the alisphenoid a straight posterior border may well be correct. Considering the great variability in the skulls at hand, absence of the structure in some individuals is to be expected. Variable are the position of the origin in the alisphenoid margin and, particularly, length and posterior connection of the spine. These are practically never the same on right and left sides. The direction of the spine

is, apparently, always straightly posterior and approximately horizontal.

The Oligocene tayassuine *Perchoerus* has a foramen ovale completely encircled by bone (Pearson, 1923, p. 79). The Recent tayassuines have no foramen ovale. They have an alisphenoid spine similar to that found in the suids, but better developed. In many *Tayassu* the spine of the alisphenoid is on one side so long that it touches the auditory bulla, that is, completely bridges the foramen lacerum. A complete bridge is rare in *Sus* and other suinae. Rather, a short process, sometimes merely emphasizing a notch, seems to be the rule. Formation of a complete bridge results from the development of a short process extending forward from the bulla and meeting that from the alisphenoid. The tips of these two processes were also seen not in contact, and in some cases not exactly opposite each other; but it seems that in life they are always connected by a tough ligament.

It follows that the alisphenoid in the extant Suina has lost the foramen ovale found in the ancestral forms. Some Suina have instead developed one or two osseous spines which, posterior to the alisphenoid plate, separate the mandibular nerve exit from the rest of the foramen lacerum.

Such secondary subdivisions of cranial foramina have previously been described as occasional variations in *Homo,* developed in the hypoglossal foramen (Lillie, 1917, p. 133) and in the posterior lacerum area, the jugular foramen (Hayek, 1929; also *Lama* and *Meles,* p. 70). In man, processes backward from the petrosal and forward from the occipital bone can divide the jugular foramen partly or completely; instead of the usual one there can be 2, 3, or 4 openings; but, apparently in contrast to our observations in pigs, these variable divisions separate nerves and vessels in extremely variable ways.

Thorpe, in his monograph of the suiform infraorder Oreodonta (1937), incidentally mentions phylogenetic loss of the foramen rotundum. He records both presence and absence in late Oligocene *Leptauchenia* (p. 240 and 258); a small opening on the left and none on the right side in a late Oligocene *Eporeodon* (p. 68); absence in other late Oligocene and in an early Miocene individual of that genus (pp. 69, 77, 88); and absence in late Miocene *Ticholeptus* and all later oreodonts (p. 191). As regards the foramen ovale, a glance at the literature and random study of a few specimens gave the impression that it was preserved in the Oreodonta throughout their late Eocene to Middle Pliocene history. This may well be true in general. However, the fact of intrageneric variability of foramen ovale occurrence is particularly well illustrated in oreodonts, presumably because their Oligocene crania have been found in rather large numbers. The foramen ovale is mentioned by Thorpe as present in *Leptauchenia* (p. 221), and as large in a later form, the early Miocene *Merychyus* (p. 230). He found it large in a Middle or Upper Oligocene *Eporeodon* (p. 69), small in an Upper Oligocene individual (p. 88), very large in one from the Lower Miocene (p. 77). Professor John Clark noticed that in many of the numerous late Oligocene *Eporeodon* crania in the Carnegie Museum, Pittsburgh, the foramen ovale is of normal size on one side while tiny or absent on the other side (oral communication).

Perissodactyla

In the surviving forms of the perissodactyl superfamilies Equoidea, Tapiroidea and Rhinocerotoidea, the mandibular nerve passes from the cranium within the foramen lacerum; it emerges through an orifice in the tough membrane closing this large basicranial gap, between the orifices for the internal carotid and middle meningeal arteries. The absence of a foramen ovale is, however, not characteristic either of the three surviving groups as a whole or of the two extinct branches of perissodactyls, Brontotherioidea and Chalicotherioidea.

The innumerable ventral views of brontothere skulls in Osborn's comprehensive monograph (1929) show the separate foramen ovale in almost every case. Examples from three Middle Eocene genera are figures 250, 262, and 278; four of the Upper Eocene genera are shown in figure 324, and six of the Lower Oligocene genera in figure 393. The few plate figures in which the fofamen ovale can not be seen apparently

show skulls with matrix or disturbances in the basicrancial region. Every brontothere skull we studied (Eocene and Oligocene, A.M.N.H. and M.C.Z.) does have a foramen ovale at quite a distance from and in front of the lacerum. Thus it seems that when the Brontotherioidea became extinct early in the Oligocene, they still had what we must now regard as the primitive ungulate pattern of mandibular nerve exit.

The foramen ovale of the late Miocene *Macrotherium* is indeed part of "the typical chalicotherine arrangement of its basicranial foramina" (Colbert, 1934, p. 378). The foramen is also conspicuously distinct from the lacerum in the two other branches of the chalicotheres, at least in the unique skull (A.M.N.H. 5096) of the late Eocene eomoropine *Eomoropus* and in the many skulls known of the early Miocene schizotherine *Moropus*. The various descriptions of *Moropus* skulls do not specifically mention this; but, remembering that perissodactyl and artiodactyl alisphenoids are supposed to be basically different, we may note that for Holland & Peterson the antero-external border of the foramen lacerum in *Moropus* "recalls what is found in the skull of the bison" (1914, p. 238).

The variable condition of the foramen ovale in the most primitive equid genus, *Hyracotherium,* has been described above. The only known adult skull of *Orohippus* (A.M.N.H. 12648) is incomplete and crushed. In the right alisphenoid there are several cracks, parts of which could be foramina. In the left alisphenoid a large subquadrangular gap, whose anterior border is apparently natural, is located just posterolateral to the posterior opening of the alar canal, suggesting the presence of a foramen ovale in this area. The posterior border of this gap is located from 9 to 11 mm. anterior to the well preserved anterior border of the foramen lacerum. In a relatively well preserved juvenile *Orohippus* skull (U.S. N.M. 17835) a separate foramen ovale is apparently absent. No specimen of *Epihippus* has the basicranial region preserved. Numerous specimens of *Mesohippus, Miohippus, Merychippus,* and *Pliohippus* in the American Museum have been examined and all are essentially like *Equus* in the arrangement of their cranial foramina. None of these later Equidae has a foramen ovale. The exit of the mandibular nerve may be marked by a notch of variable depth in the anterior border of the foramen lacerum, the incisura ovalis (fig. 1 B). Usually, we found, this is not the case (fig. 1 A).

In the earliest of Tapiroidea of which a skull is known, an extensive bone bridge separates the foramen ovale from the lacerum (early Eocene *Heptodon,* M.C.Z. 17670, to be described by H. Seton). In one of the only two *Protapirus* skulls ever found in the American Middle Oligocene, Hatcher did mention a foramen ovale in the alisphenoid, however, "at the base of the pterygoid" (1896, p. 165). The respective opening is shown in Hatcher's figure (pl. II, fig. 3). It is not a foramen ovale; it corresponds exactly to the posterior opening of the alar canal in the extant tapirs. Actually in the Oligocene form the mandibular nerve exit had become included in the foramen lacerum. This condition is well known in *Tapirus* (e.g., van Kampen, 1905, p. 579). Not previously noted, apparently, are variations of the foramen lacerum in *Tapirus.* Its anterior margin is a straight transverse line, as in van Kampen's figure 65, only in some tapir skulls. In others there are two or three notches. *Tapirus indicus* M.C.Z. Mammal Department 6347 may be mentioned as one example of the variations our *Hyracotherium* specimens had led us to expect. On its right side, a posteriorly projecting spine from the sphenoid divides the foramen lacerum anteriorly into a narrower median and a wider lateral section. On the left side two spines produce the three incisures sometimes present in horse skulls, but they are much more pronounced here. The middle notch clearly corresponds to the incisura ovalis of

horses. It extends farther forward into the alisphenoid than that medial to it (lodging the internal carotid), and the lateral notch (middle meningeal artery) is so long that its front margin is only 3 mm. distant from the posterior opening of the alar canal. This distance is 21 mm. on the right side of this skull.

More than half a century old but apparently overlooked or forgotten is Osborn's following observation. A "very characteristic feature of rhinoceros skull evolution (is) the progressive confluence of the foramen ovale with the foramen lacerum medium, which can be observed in all stages from the Oligocene to the Miocene types" (1898, p. 119). The six specimens in which Osborn described and figured the still-separate foramen ovale are representatives of only the Middle Eocene genus *Hyrachyus* and the Oligocene genera *Subhyracodon* and *Amphicaenopus*. It seems necessary to cite more cases to obtain general recognition for Osborn's discovery.

We have seen the foramen ovale well-formed in numerous Middle Oligocene rhinoceros skulls such as *Subhyracodon* A.M.N.H. 12452 and *Caenopus* A.M.N.H. 552, M.C.Z. 3370 and 3371. In both *Hyracodon* M.C.Z. 6608 and 6638 it is a narrow slit on one side, but this may be a postmortem condition. No foramen ovale was found in either *Metamynodon* A.M.N.H. 547 (Scott, 1941, pl. XCII, fig. 1) or *Metamynodon* M.C.Z. 9157. In a basal view figure of the latter specimen (Scott and Osborn 1887, fig. 9) the area, which is somewhat warped on both sides, appears to be basically different on the left (the lettering "fov" pointing to part of the lacerum) and the right (separate foramen ovale). Actually there is no separate foramen ovale on either side, but on the right side there is a trace of a backward spine in about the middle of the anterior border of the foramen lacerum. One is tempted to connect the larger size of *Metamynodon* skulls with their lack of a foramen still present in smaller contemporary relatives; but then one must remember that of the two extant Camelinae it is the larger genus which has retained the foramen.

The late Oligocene or early Miocene *Baluchitherium* skull A.M.N.H. 18650 has three shallow notches in the posterior margin of the alisphenoid, just as in horses; and, as in horses and the extant rhinoceroses, there is no foramen ovale. The canal labeled "for. ov. (V^3)" on pls. I–II by Granger and Gregory, 1936, slopes too strongly forward and opens on the outside too far anteriorly. It appears to be, rather, the foramen rotundum for nerve V^2.

The ovale is still a separate foramen in the early Miocene *Diceratherium* (in all skulls figured in ventral view by Peterson, 1920). Among the late Miocene and early Pliocene rhinoceros genera the foramen ovale has become a rare feature. In *Teleoceras*, Osborn (1890, p. 94) found that "The foramen ovale is either confluent with or separated by a slender ridge of bone from the foramen lacerum medium." It is confluent, i.e. absent as a separate structure, in the three *Teleoceras* skulls we studied (A.M.N.H. 8385, M.C.Z. 4446 and 12184). The four skulls of *Chilotherium* figured in ventral view by Ringström (1924) apparently do not have it. In another *Chilotherium* skull (fig. 3) a thin bone lamina completely separates from the large foramen lacerum a small oval foramen. This was briefly mentioned as a separate foramen ovale (Edinger, 1937), but in the present context it becomes a rather interesting detail. The small right and left foramina are different both in shape and position. The left one is almost entirely lateral and the right one also extends only in part, though more than the left, anterior to the foramen lacerum. This appears to be the mandibular nerve exit in the last stage of its, so to speak, backward migration into the foramen lacerum.

No extant rhinoceros has a foramen ovale. They are still another group in which there can develop that extremely

FIG. 3. Late Miocene perissodactyl, *Chilotherium habereri*. Outlines of posterior part of endocranial cast, ventral view. Black: endocasts of the foramina ovale, lacerum, hypoglossi. After Edinger. × 5/12.

variable backward spine from the alisphenoid which may be a structure serving to replace in individual ontogeny the osseous wall of the mandibular nerve lost in phylogeny. The anterior section of the foramen lacerum is an enormous gap in the basicranium. Its margins are smooth bone in *Rhinoceros* (A.M.N.H. 54456). A short spine juts back into it in *Diceros* no. 139693. In *Ceratotherium* 5192 there is in place of this spine an obliquely longitudinal thin bridge, externally separating the prootic area of the foramen lacerum into about a lateral third and median two-thirds. A similar bridge is developed in *Dicerorhinus* M.C.Z. 6346; here the lateral section of the foramen is 8 mm. wide on one side and 10 mm. on the other, the median sections being 5 and 8 mm. wide, respectively.

CONDYLARTHRA

The preceding survey of the surviving ungulate orders, each containing many forms without foramen ovale, suggests that originally the Ungulata *s.l.* were provided with this foramen. If its presence is indeed a primitive feature in ungulates, it should have existed in the Condylarthra, the "broadly structurally ancestral group" (Simpson, 1945, p. 233) of Paleocene and Eocene protungulates which must have contained the ancestors of Artiodactyla and Perissodactyla. Very few condylarth specimens have the respective area satisfactorily preserved; but those we saw or read about all conform with our expectations.

A complete and uncrushed lower Eocene specimen of the phenacodontid *Phenacodus* (P.U. 14864) shows a small foramen ovale located just posterolateral to the posterior opening of the alar canal. It is separated from the foramen lacerum by a broad plate of bone.

Cope stated that in the late Paleocene *Periptychus* "The foramen ovale is not separated from the meatus auditorius below" (1884, p. 388). We were not able to clarify this mysterious remark. In Cope's specimen (A.M.N.H. 3669) the area is too cracked and incomplete, and there is apparently no other specimen that yields information in this respect. In one of the three specimens of the late Paleocene *Pleuraspidotherium*, all of which are crushed, the separate foramen ovale was found (Pearson, 1927, p. 453, fig. 51).

The ovale of the early Eocene genus *Meniscotherium* was described by Cope (1884) as "scarcely separated from the foramen lacerum anterius" (p. 494), and as "not cut off from the foramen lacerum" (p. 499) in the specimen A.M.N.H. 4412. In this specimen we cannot make out the foramen lacerum but distinctly see the foramen ovale fully encircled by the sphenoid wing. Correspondingly, the endocast preparation A.M.N.H. 48082 shows a small downward stone column, representing the mandibular nerve. In the excellently preserved cranium A.M.N.H. 4447 (fig. 4) the foramina bear a remarkable resemblance to those of the ?eohippus specimen mentioned above. Not only is the foramen ovale set off from the lacerum by a bone bridge 3–4 mm. broad (or, rather:

high); the foramen at its ventral rim measures 2 × 3.5 mm. in ?*H.* and in this *Meniscotherium;* further, the distance between ovale and rotundum is 9 mm. in both specimens.

Some Non-Ungulate Mammals

The ungulate and protungulate data assembled above illustrate two phenomena. 1) Contrary to current opinion, the relations between mandibular nerve and sphenoid bone can vary within groups at least as small as genera. 2) In the early Tertiary, the mandibular nerve generally passed through a foramen ovale. It is in later forms that the nerve frequently used the foramen lacerum for its passage from the braincase. Some branches of the ungulate stock during Tertiary times lost the foramen. This fact, too, is at variance with a concept held by students of modern forms. Neontologists regard the foramen ovale as secondarily developed within the evolution of the mammalian orders.

1) "The exit of the mandibular nerve is in the anterior section of the foramen lacerum . . . or it becomes walled off from this gap; this gives rise to the foramen ovale" (Haller, 1934, p. 576). *2*) M. Weber & de Burlet also regard the prootic cleft as the original exit of the third branch of the trigeminal nerve. They state further that when and where the alisphenoid expanded in correlation with progressively expanding brain volume, "the V^3 *gradually came to lie* within the alisphenoid; in many mammals, however, the foramen ovale has *not yet* become separated from the foramen lacerum" (1927, p. 64). *3*) Hecker & Grünwald concluded from their survey of extant mammals that "The pressure of the enlarged brain enforces ossification more and more complete, and this separates the cranial foramina from each other" (1926b, p. 363), "so that man has the largest number of individual orifices" (p. 361). *4*) A. Weber's study on "evolution of the foramen ovale" had arrived at similar conclusions. He used skulls of two genera of monkeys, of the apes, and of various races of man. He reports four different types of foramen ovale, ranging from open notch to completely closed foramen, none of them restricted to one group. He nevertheless concluded that, with regard to the foramen ovale, "gibbon, chimpanzee and gorilla have attained a degree of evolutionary development equal to that of the human races regarded as the most civilized" (1907, p. 238). *5*) Stadtmüller (1936) supports the same theory with examples of higher and lower orders of mammals. "The prootic gap apparently is the primitive passage of the inframaxillary (third) branch of the trigeminal nerve. This is *still* the condition in, for example, rodents, etc." (p. 919). "The foramen ovale is a separate entity as a rule in primates and carnivores, the nerve *having come to lie* within the alisphenoid through expansion of this element . . . corresponding to the increasing brain mass. It is fused with the foramen lacerum anterius (medium) in the majority of rodents, some ungulates, and cetaceans" (p. 912. All italics are ours.)

It seems that the foregoing theory is based upon two kinds of data to which neobiologists attribute phylogenetic significance. The first is embryological data. In the mammalian embryo, the semilunar ganglion of the trigeminal nerve develops outside the skull anlage. Its intracranial position and the three intracranial nerve roots extending from it therefore are indeed secondary in ontogeny, as is also the separation of the cranial foramina from each other. The

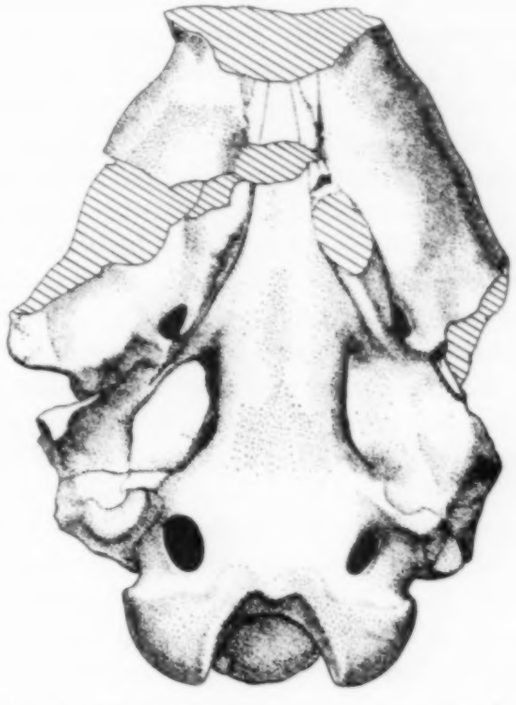


Fig. 4. Early Eocene protungulate, the condylarth *Meniscotherium.* Cranial fragment, ventral view (A.M.N.H. 4447). Black: foramina ovale, lacerum, hypoglossi. × 1⅔.

foramen ovale of the newborn human is still merely a gap in the posterior border of the sphenoid. Secondly, neontologists have not always resisted the temptation to draw conclusions regarding details of phylogeny from comparisons of living animals.

As the phylogenetic development of the mammalian orders has gone separate ways for some 70 million years, paleontologists cannot envisage any series of conditions in Recent mammals as a series of steps in evolution. There is, of course, the possibility that the conditions in Recent forms may shed light upon the general course of evolution. In the present case, however, this cannot be conceded.

An examination of the passages quoted above from the neomammalogical literature itself reveals that the neontological conclusions regarding the evolutionary change in the position of exit of the mandibular nerve are unwarranted. The Paleontological data on the orders named in these quotations clearly support the view that the foramen ovale is an original character of the Mammalia as a whole, and that in some branches a trend developed to abolish this separate cranial exit of the mandibular nerve.

According to the handbook cited above as no. 5, Primates are one of the two orders of higher mammals generally distinguished by the possession of a foramen ovale. The special study we quote as no. 4 contradicts this. The later literature adopted only its general, "evolutionary" conclusions. We, however, see in that paper a report on considerable variability of the foramen ovale in Recent higher primates. Within, for example, the species *Homo sapiens* occur the types we found in the second and third of the Eocene specimens mentioned in the Introduction, and types transitional between these two. Listing examples for the four stages he distinguished in his material, A. Weber named, among others: with open notch instead of foramen, *Semnopithecus,* Australians, New Guineans; incompletely closed notch, *Macacus,* New Guineans; foramen ovale closed by one spine, *Hylobates,* Australians, New Guineans; foramen ovale closed by two coalesced beams, *Hylobates,* Europeans (1907, p. 237).

In the other order cited as having a foramen ovale, Carnivora, we know indeed of no skull, fossil or Recent, in which the foramen is not fully formed. Apparently the trend towards its loss, noted in several branches of the ungulate orders, never developed in this other still flourishing order of the cohort Ferungulata.

The following instance is possibly significant with regard to the preservation of the foramen ovale in both carnivores and primates. In both orders, this foramen contains, besides the mandibular nerve, a branch of the internal maxillary artery. This is the middle meningeal artery in all Recent carnivores (Story, 1951, p. 513). According to human anatomy textbooks, the vessel accompanying the mandibular nerve in man is a smaller branch, the ramus meningeus accessorius. The ungulate foramen may never have had such double function. Today, at least, the middle meningeal artery enters the skull in the foramen lacerum both in ungulates which have a foramen ovale (*Bos:* Sisson, 1937, p. 721) as in those without (*Sus, Equus*). It must be noted, however, that entrances of the smaller cranial arteries are also, like mandibular nerve exits, not fixed ordinal characters.

The Rodentia constitute an order whose members either lack or have a foramen ovale. In both cases Hill found the mandibular nerve accompanied by "a small artery, a branch of the internal maxillary artery" (1935, p. 126). Hill's material included *Rattus;* but in the material used for Greene's detailed description of rat anatomy the foramen ovale apparently served only the mandibular nerve (1935, legend to fig. 9, and chapters on cranial nerves and on cranial vessels).

"The majority of rodents" are cited as "still" not having a foramen ovale. No basis for this statement was found in the literature, and it would indeed be too big a task to study the condition in an order containing hundreds of genera.

Hill lists (1935, p. 121) the 18 Recent

genera in which he studied the cranial foramina, and (p. 126) the 8 genera in which he found the foramen ovale confluent with the foramen lacerum, that is, situated between alisphenoid and tympanic bulla. The other 10 genera have a distinct foramen ovale in the alisphenoid.

When one sorts taxonomically the material of Hill's anatomic study, even these few representatives of a particularly vast order serve to illustrate foramen ovale variability. The genera with distinct foramina belong to 3 families each of the suborders Sciuromorpha and Myomorpha. Those without a foramen ovale belong to the same suborders, *Geomys* and *Thomomys* even to the same subfamily (Geomyinae) as a form having the foramen (*Cratogeomys*). *Erethyzon*, the only genus of the suborder Hystricomorpha represented in Hill's sample, is listed among the forms without a separate foramen ovale. A peculiar condition is described in another hystricomorph rodent; in a *Myocastor* skull the exocranial opening of the mandibular nerve passage is in the foramen lacerum, but endocranially there is a foramen ovale confluent with the foramen rotundum. This is incidentally reported (p. 1355) in Hecker and Grünwald's (1926) survey of foramen rotundum conditions in extant mammals, a paper which makes one wonder how great a variation would be found in the foramen ovale if it were made the subject of a similar comparative investigation.

Castor is one of the Recent sciuromorphs which lack a foramen ovale. Fossil Castoridae show that this is not true of the family as a whole. Olson (1940) studied four castorid genera forming a time series and very probably an ancestral-descendent series from Miocene to Recent. The fossil skulls have, with two exceptions, no foramen ovale. The two skulls having the mandibular nerve exit enclosed in the sphenoid wing are among those of the oldest form of the series, the early Miocene *Palaeocastor* (Olson, 1940, fig. 3 A). Of the two still older, Oligocene castorid genera there apparently exists no specimen with the respective region satisfactorily preserved. The sphenoid wing is usually broken in the delicate skulls of small fossil rodents. One cannot, therefore, exclude the possibility that the distinct foramen in two *Paleocastor* was a phylogenetically unimportant variation. But its presence in only the oldest of the forms studied by Olson is highly suggestive of evolution parallel to that we observed in ungulates, that is, early presence and later loss of the foramen ovale. The idea finds support in Lavocat's identification of the foramen in all three Oligocene sciuromorph genera of which he had well preserved skulls (1951, pp. 54–55).

The Insectivora are conspicuously absent in the handbook summaries citing orders of higher mammals with a foramen ovale and orders of lower mammals without it. Indeed, if presence and absence of this foramen really were ordinal characters, the order which has remained the most primitive of all the Eutheria would have to be classified with the higher orders. Muller, in her comprehensive description of the cranial foramina in Recent Insectivora (1934), noted a foramen ovale well within the sphenoid wing in every one of the many species studied, except in Soricidae. Its occurrence in the overwhelming majority of the least progressive placentals is, to us, another indication of its primitive nature. Muller, like the other neontologists, regards the absence of a foramen ovale, the exceptional condition among insectivores, as primitive because in soricids the alisphenoid has a primitive character and because a foramen ovale not encircled by bone agrees with the cranial anlage. "A foramen ovale *not* located on the outer side of the alisphenoid . . . probably dates from the *secondary* mammalian period" (p. 243; italics ours). But one need not go further back than the Pleistocene to see that, on the contrary, the lack of a foramen inside the alisphenoid in extant soricids is a second-

ary development. The recent Soricidae probably are surviving relatives of the Pleistocene Nesophontidae (Simpson, 1945, p. 177), and these do have the foramen (Anthony, 1916, pl. XXIII, fig. 3; two other skulls: Anthony 1918, fig. 17).

Recent material alone, namely the extant Insectivora, contradicts not only the theory of secondary acquisition of the foramen ovale within mammalian orders, but also the assumption, quoted above, concerning the cause of foramen ovale appearance in higher mammals. Not "expansion of the brain," but of the cerebral hemispheres indeed took place in the evolution of many branches of the Mammalia. This trend, however, never developed in the known history of the Insectivora practically all of which, nevertheless, have the foramen. Further, the cerebra of the ox and the horse are quite similar, yet the two forms are extremely dissimilar with regard to the osteology of the mandibular nerve exit. Paleontological material most definitely shows that expansion of the cerebrum did not cause the foramen ovale to appear within mammalian phylogenies. For example, a considerable number of endocranial casts has recently been assembled which illustrate brain evolution in the major branches of the Perissodactyla (Edinger, in preparation). Hence we know the brains of the early and middle Eocene perissodactyls in which the foramen ovale was present. They are primitive and slender. In the modern perissodactyls, with greatly expanded cerebra, the foramen has disappeared.

There are indeed no fossil data known which show the presumed appearance of the foramen ovale as a secondary development within the history of the various branches of Mammalia.

Considering the variations of the mandibular nerve exit and the obvious insignificance of the nerve's cranial relations for its function, the postulated "forward" shift of the nerve root into the sphenoid area can of course have occurred just as well as the shift observed, "backward" to the posterior margin of the bone. One can even imagine, and may find if more material is studied, loss and reappearance of the foramen ovale within the history of mammalian groups. The cases of loss within mammalian phylogenies themselves become cases of acquisition and loss if one takes into consideration the reptilian prehistory of the Mammalia.

Pre-Mammalian Trigeminal Nerves

Comparing mandibular nerve exits in Recent mammals with those of their extinct ancestors, we have found in several groups the separate passage type more frequent the further back we went in their evolutionary histories. A glance at trigeminal nerve exits in reptiles suggests that the foramen ovale was acquired at the origin of the class Mammalia. No comparable structure exists or existed in the Reptilia.

Trigemino-cranial relations in Reptilia are amply described in both neo- and paleo-zoological literature, as are their differences from the respective conditions in the descendant class, Mammalia. Discussion, however, appears to be concerned only with the osteological problems of the area. It is true that the organ enclosed by and shaping much of the cranium has been taken into consideration. As mentioned above, the phylogenetically enlarging cerebrum was regarded as the main cause for the change from the generally slender ascending process of the reptilian epipterygoid into the larger mammalian alisphenoid which came to enclose nerves V^2 and V^3. The trigeminal nerve itself, however, figures in the debate only as an aid in seeking the exact homology of the reptilian bone which lies anterior to the entire nerve or to V^{2-3}. No one, as far as we know, has taken account of a neurological circumstance, a difference between reptiles and mammals which must have been intimately related to the evolutionary appearance of the foramina rotundum and ovale. This is

the structure of the proximal portion of the trigeminal nerve. At its passage through the cranial wall the reptilian trigeminal is not three-pronged as in mammals. Either nerves V^1, V^2 and V^3 leave the brain chamber as one trunk, or they are forked into two branches, the ophthalmic and the maxillo-mandibular.

One foramen trigemini is regarded as the primitive condition in reptiles. In the lower vertebrates generally the trigeminal trunk passes outward through one orifice, the prootic cleft of the cranium, splitting into three branches below the cranial base. This is the condition in *Sphenodon* and also in crocodiles.

Two foramina are suggested by Wettstein's description of the latter, "Passage from the cranial cavity of the ophthalmic ramus through a separate foramen, separated from the foramen trigemini by the laterosphenoid" (1937, p. 313). The endocranial wall, however, has only one large orifice (see Gregory and Noble, 1924, fig. 2 A). The epipterygoid spicule developed between V^1 and V^2 is an extracranial structure which, foramen- or canal-like, shields the ophthalmic ramus at the beginning of its extracranial forward course (ibid., fig. 2 B; de Beer, 1926, fig. 92).

In the majority of extant Reptilia the ophthalmic so diverges from the main trunk that it emerges at the anterior, instead of the posterior border of the epipterygoid. Such a course is assumed in some fossil reptiles; but where the nerves themselves have vanished and only foramina can be studied, one can not reliably state whether the V^1 emerged with V^2-V^3 or with the other eye muscle nerves, nor whether some small anterior foramen or notch served nerve V^1 or a blood vessel. For our present problem the important point is only the common emergence from the osseous cranium of V^2 and V^3 in reptiles, fossil and Recent.

A few fossil specimens indicate that the maxillo-mandibular split began to develop within the class Reptilia. These specimens belong to three families of the therapsid infraorder Cynodontia. Early and Middle Triassic in age, they represent individuals at a time in the history of Reptilia, and of a branch of that class, which were close to the origin of mammals. The condition of their foramen trigemini is noteworthy also as one more indication of the gradualness of the reptile-mammal transformation. Among the therapsid crania which have been prepared or sectioned so as to reveal prootic and epipterygoid, incipient division of the trigeminal foramen is exceptional.

1) In *Cynognathus* (*berryi*, Lower Triassic), a mammal-like reptile with a broad, fan-shaped epipterygoid resembling an alisphenoid, Broom discovered that "Between the alisphenoid and the prootic are two large oval foramina" (1911, p. 905). Broom's figure of the specimen (pl. XLVI, fig. 1) however shows only one opening in the suture between the two bones, the other being antero-dorsal to it and quite within the "alisphenoid." Thus the speculation was warranted that the anterior orifice enclosed the maxillary nerve, that is, that a foramen rotundum had developed in this reptile parallel to the later development in mammals. Because Broom's figure gave rise to this repeatedly published idea (Gregory & Noble, 1924, p. 454; Versluys, 1936, p. 757), it must be noted here that according to a later study of the specimen (Haughton, 1922) there are not two small foramina but there is only one (p. 305). This lies in the suture. However, it extends forward into the epipterygoid margin in an upper and a lower notch (pl. XIII, fig. 7). Very probably these notches indicate the positions of V^2 and V^3, and thus, possibly, the beginning of a split of the maxillo-mandibular trunk within the foramen trigemini.

2) Among the many therapsid crania studied in serial sections by E. C. Olson, similar incipient division of the trigeminal foramen was seen in several *Thrinaxodon* of the early Triassic (oral communication).

3) The braincase of a later, Middle Triassic "Unidentified cynodont . . . which compares closely with the *Trirachodon* remains with which it is found" has two foramina in the prootic-epipterygoid suture (Parrington, 1946, p. 190; left side view, fig. 7 A; to judge from fig. 7 B, the right side has the normal single foramen trigemini). The upper foramen appears to have been the exit of the maxillary nerve which had intracranially separated from the mandibular nerve. It is indeed regarded by Parrington as a foramen rotundum, the lower foramen as a foramen ovale (p. 190). The margin of the upper foramen is in great part formed by the epipterygoid. Even so, both maxillary and mandibular nerves passed outward in the suture.

Thus Broom's (1911) statement still holds true, and of the Reptilia as a whole: "In the mammal the alisphenoid differs from that of the Cynodont mainly in having the 2nd and 3rd branches of Nerve V. passing through instead of behind it" (p. 992). Olson's comprehensive investigation of therapsid crania likewise found the epipterygoid never perforated, not even in those forms in which it is so expanded as to make it very similar to an alisphenoid (1944, p. 112). There is also only one, a post-epipterygoid trigeminal foramen in the late Triassic and Jurassic mammal-like reptiles *Bienotherium* (Young, 1947, fig. 3) and *Olygokyphus* (Kühne, 1952, p. 62, p. 67). Thus from all the material now known one must conclude that the trigeminal nerve root is not threepronged in Reptilia; and, while the foramen trigemini of some cynodont therapsids suggests a beginning and even a completed separation of the maxillary and mandibular branches of the nerve, their exit was generally as one stem even in the most mammal-like forms.

The fact that in some therapsid reptiles the epipterygoid bone had already expanded to the proportions of a mammalian alisphenoid is another instance in the record of evolution casting doubt on the neontological concept. It is assumed that the alisphenoid enlarged (and came to enclose the trigeminal nerve roots) in relation to the increase of relative brain size in the mammalian orders. Actually, we see, expansion of the bone was well on its way in therapsids, that is, when the brain at least in the sphenoid bone area was still reptilian in type. The data of paleoneurology further show that the earliest mammals did not have cerebra so spectacularly larger than their reptilian forbears as that theory presupposes. Olson's comparisons of mammal-like reptiles with mammals indicated "that the expansion of the alisphenoid has been entirely posterior" (*loc. cit.*). Thus when the outward maxillo-mandibular portion of the trigeminal nerve became a forward-downward maxillary branch and a sideward-downward mandibular branch, their exits had come to lie in the alisphenoid area and created two new foramina.

One must assume that the intracranial split of the nerve and consequent development of foramen rotundum and ovale occurred at or near the time of the origin of mammals. The record, unfortunately, does not go farther back than to the earliest Tertiary. The lacerum-ovale area is not well preserved in any of the tiny, fragmentary Mesozoic mammal skulls described in the literature. Only in a late Jurassic *Triconodon* could Simpson very tentatively regard as a foramen ovale a paired opening which, however, is not inside the alisphenoid but "probably lay between the basisphenoid and the alisphenoid or the periotic or both" (1928, p. 85).

The fossil record is nevertheless, we believe, sufficient to show that, contrary to neontological theory, the foramen ovale was a progressive feature only during the earliest time of mammalian evolution. In the Present, therefore, the foramen ovale is a primitive feature most mammals have retained. Absence of the foramen in some extant mammals is neither the ancestral nor a primitive but a secondary condition. This has developed in forms so different from each other that one can hardly expect to find any one cause for the phenomenon.

Summary

In numerous living Mammalia (including man) a foramen ovale in the alisphenoid bone encloses the root of the mandibular nerve. Absence of this foramen in the other living Mammalia (including some lower mammals) and in the mammal embryo induced the theory that a separate mandibular nerve exit is an advanced character, developed within the evolution of some orders. Its absence in horse, rhinoceros and tapir has been regarded as one of the characters distin-

guishing the Perissodactyla from the Artiodactyla; in the latter order, presence of the foramen ovale appeared to be characteristic.

A study of the foramen ovale area in extant and extinct representatives of several orders was undertaken when we saw both types of mandibular nerve exit and an intermediate in Lower Eocene crania probably referable to one genus, *Hyracotherium*.

We found that the condition can indeed vary not only within orders but also within genera. Several types of extant artiodactyls lack the foramen as do the extant perissodactyls. In both these ungulate orders, however, a separate foramen ovale was the usual condition in the early Tertiary as it was in the ancestral order, Condylarthra. Thus in ungulates the foramen ovale is not only subject to the variability known of other cranial foramina, but there also existed in some branches an evolutionary trend for the foramen ovale to merge with the foramen lacerum. Comparisons of fossil and Recent material suggest a similar trend in certain families of the orders Rodentia and Insectivora.

The foramen ovale, consequently, is neither a constant nor an advanced character. Its absence, rather, is the secondary condition; it developed, at different times, in different phylogenies. This phylogenetic loss is at variance also with the theory which relates the origin of the foramen ovale with cerebral and corresponding alisphenoid expansion in progressive evolution. It seems more plausible to relate the formation of the foramen with an earlier paleoneurological development. In the ancestral class, Reptilia, the mandibular nerve passes and always passed from the braincase together with the maxillary nerve. Its separate cranial exit, the foramen ovale, presumably was acquired when the mandibular nerve came to branch off the trigeminal stem intracranially, during or near the origin of mammals.

Literature Cited

Adams, L. A., and S. Eddy. 1949. Comparative Anatomy. An introduction to the vertebrates. New York and London.

Anthony, H. E. 1916. Preliminary diagnosis of an apparently new family of insectivores. Bull. Am. Mus. Nat. Hist., **35**: 725–728.

Anthony, H. E. 1918. The indigenous land mammals of Porto Rico, living and extinct. Mem. Am. Mus. Nat. Hist., N.S., **2**: 332–435.

de Beer, G. R. 1926. Studies on the vertebrate head. II. The orbitotemporal region of the skull. Quart. J. Microsc. Sci., **70**: 263–370.

Broom, R. 1911. On the structure of the skull in the cynodont reptiles. Proc. Zool. Soc. London, **1911**: 893–925.

Colbert, E. H. 1933. The skull and mandible of *Conohyus*, a primitive suid from the Siwalik Beds of India. Am. Mus. Novit., **621**: 12 pp.

Colbert, E. H. 1934. Chalicotheres from Mongolia and China in the American Museum. Bull. Am. Mus. Nat. Hist., **67**: 353–387.

Colbert, E. H. 1935a. Distributional and phylogenetic studies on Indian fossil mammals. IV. The phylogeny of the Indian Suidae and the origin of the Hippopotamidae. Am. Mus. Novit., **799**: 24 pp.

Colbert, E. H. 1935b. Siwalik mammals in the American Museum of Natural History. Trans. Am. Philos. Soc., N.S., **26**: X + 401 pp.

Edinger, T. 1937. Ein Steinkern der Gehirn-, Nasen- und Neben-Höhlen von *Chilotherium*. Bull. Geol. Inst. Upsala, **27**: 32–41.

Edinger, T. 1948. Evolution of the horse brain. Mem. Geol. Soc. Am., **25**: X + 177 pp.

Edinger, T. (in preparation). Brain evolution in the Perissodactyla.

Granger, W., and W. K. Gregory. 1936. Further notes on the gigantic extinct rhinoceros, *Baluchitherium*, from the Oligocene of Mongolia. Bull. Am. Mus. Nat. Hist., **72**: 1–73.

Greene, E. C. 1935. Anatomy of the rat. Trans. Amer. Philos. Soc., N.S., **27**: XI +370 pp.

Gregory, W. K., and G. K. Noble. 1924. The origin of the mammalian alisphenoid bone. J. Morphol., **39**: 435–463.

Haller v. Hallerstein, V. 1934. Kranialnerven. Handb. vergl. Anat. Wirbelt. (L. Bolk et al., eds.), **2**, I: 541–684.

Hatcher, J. B. 1896. Recent and fossil tapirs. Am. J. Sci., (4) **1**: 161–180.

Haughton, S. H. 1922. On some Upper Beaufort Therapsida. Trans. Roy. Soc. S. Afr., **10**: 299–307.

v. Hayek, H. 1929. Ueber Teilung des Foramen jugulare. Anat. Anz., **68**: 65–70.

Hecker, P., and E. Grünwald. 1926a. Le trou grand rond. Etude d'anatomie comparée. Compt. rend. Soc. Biol., **94**: 1353–1361.

Hecker, P., and E. Grünwald. 1926b. Sur les causes déterminant l'individualisation des orifices de la partie antérieure de la base du crâne. Etude d'anatomie comparée chez les Reptiles et les Mammifères, *ibid.*: 1361–1363.

Hill, J. E. 1935. The cranial foramina of rodents. Jour. Mamm., **16**: 121–129.

Holland, W. J., and O. A. Peterson. 1914. The osteology of the Chalicotherioidea. Mem. Carnegie Mus., **3**: 189–406.

Hürzeler, J. 1936. Osteologie und Odontologie der Caenotheriden. Abh. schweiz. paläont. Ges., **58**, no. 3: 1–112.

van Kampen, P. N. 1905. Die Tympanalgegend des Säugetierschädels. Morphol. Jahrb., **34**: 321–722.

Kühne, W. G. 1952. The tritylodont reptile *Oligokyphus*. Diss. Bonn.

Lavocat, R. 1951. Revision de la Faune des mammifères oligocènes d'Auvergne et du Veley. Paris (Sciences et Avenir), 153 pp.

Lillie, R. D. 1917. Variations of the canalis hypoglossi. Anat. Rec., **13**: 131–144.

Muller, J. 1934. The orbitotemporal region of the skull of the Mammalia. Arch. néerl. Zool., **1** (1935): 118–259.

Olson, E. C. 1940. Cranial foramina of North American beavers. J. Paleont., **14**: 495–501.

Olson, E. C. 1944. Origin of mammals based upon cranial morphology of the therapsid suborders. Geol. Soc. Amer., Spec. Papers, **55**: 136 pp.

Osborn, H. F. 1890. Preliminary account of the fossil mammals from the White River and Loup Fork formations, contained in the Museum of Comparative Zoology. II. Perissodactyla. Bull. Mus. Comp. Zool., **20**: 87–100.

Osborn, H. F. 1898. The extinct rhinoceroses. Mem. Am. Mus. Nat. Hist., **1**: 75–164.

Osborn, H. F. 1929. The titanotheres of ancient Wyoming, Dakota, and Nebraska. I–II. U. S. Geol. Surv., Monogr. **55**.

Parrington, F. R. 1946. On the cranial anatomy of cynodonts. Proc. Zool. Soc. London, **116**: 181–197.

Pearson, H. S. 1923. Some skulls of *Perchoerus* (*Thinohyus*) from the White River and John Day Formations. Bull. Am. Mus. Nat. Hist., **48**: 61–96.

Pearson, H. S. 1927. On the skulls of Early Tertiary Suidae, together with an account of the otic region in some other primitive Artiodactyla. Phil. Trans. Roy. Soc. London (B), **215**: 389–460.

Peterson, O. A. 1920. The American dicerathères. Mem. Carnegie Mus., **7**: 399–456.

Ringström, T. 1924. Nashörner der *Hipparion*-Fauna Nord-Chinas. Paleont. Sin. (C) **1**, fasc. 4: pp. 1–158.

Scott, W. B. 1941. The mammalian fauna of the White River Oligocene, V. Perissodactyla. Am. Philos. Soc., Trans., N.S., **28**: 747–980.

Scott, W. B., and H. F. Osborn. 1887. Preliminary account of the fossil mammals from the White River Formation, contained in the Museum of Comparative Zoology. Bull. Mus. Comp. Zool., **13**: 151–171.

Simpson, G. G. 1928. A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum. London (British Museum, Natural History).

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bull. Am. Mus. Nat. Hist., **85**: XVI + 350 pp.

Sisson, S. 1938. The Anatomy of Domestic Animals. Third ed., rev. by J. D. Grossman. Philadelphia & London.

Stadtmüller, F. 1936. Kranium und Visceralskelett der Säugetiere. Handb. vergl. Anat. Wirbelt. (L. Bolk *et al.*, eds.), **4**: 839–1016.

Thorpe, M. R. 1937. The Merycoidodontidae. an extinct group of ruminant mammals. Mem. Peabody Mus. Nat. Hist., **3**, pt. IV, XXII + 423 pp.

Versluys, J. 1936. Kranium und Visceralskelett der Reptilien. Handb. vergl. Anat. Wirbelt. (Bolk), **4**: 699–808.

Weber, A. 1907. Le trou ovale du sphénoïde chez les singes et chez l'homme. Compt. Rend. Soc. Biol. Paris, **63**: 236–238.

Weber, M., and H. M. de Burlet. 1927. Die Säugetiere. Einführung in die Anatomie und Systematik der recenten und fossilen Mammalia. 2nd ed. I. Anatomischer Teil. Jena.

Weber, M., and O. Abel. 1928. Die Säugetiere. Einführung in die Anatomie und Systematik der recenten und fossilen Mammalia. II. Systematischer Teil. Jena.

v. Wettstein, O. 1937. Crocodilia. Handb. Zool., **7**, I: 237–320.

Young, C. C. 1947. Mammal-like reptiles from Lufeng, Yunnan, China. Proc. Zool. Soc. London, **117**: 537–596.

NOTES AND COMMENTS

ANIMAL FORMS AND PATTERNS [1]

DEAN AMADON

This discourse on the significance of form and pattern in animals as correlated with acuity of vision and with general level of "cerebralization" should be of great value to all students of general evolution. Portmann has a very keen eye for sequences of evolution that, in the final analysis, must be interpreted in relation to changing levels of mental organization and development of sense organs. In the mollusks, for example, beginning with the lowly oyster one eventually reaches, in the octopus, a creature with good vision and what may, without wincing, be called a brain. What a tremendous physical transformation accompanies this long evolutionary story. The shell, so dominant in the lower mollusks, dwindles and in some cases becomes an internal supporting rod, or disappears entirely; at the same time the animal gradually gets a head to accommodate its brain and eyes! Or another example: some physiologists, noticing that spermatogenesis in mammals with an external scrotum takes place at a lower temperature than that existing in the body cavity, have been naive enough to suggest that this is *why* the testes are external. Doubtless, many like myself somehow sensed that this was to put the cart in front of the horse, but it remained for Portmann to point out that greatest development of an external scrotum occurs in mammals where vision is dominant, and that it is often accompanied by other visual embellishments of the "reproductive pole," such as the gaudy posteriors of some primates, in one of which the scrotum itself is bright blue. These external signals of masculinity, in the species where they occur, have selective value in determining social rank and reproductive status. Physiological adjustments, as in the lowering of the scrotal temperature, are purely secondary.

Although Portmann is entirely correct in emphasizing that we must study "natural history" to learn *why* animals have various forms and color patterns (the physiologist and geneticist can only tell us *how* the structures are formed), he is not entirely familiar with the recent evolutionary emphasis on selection, nor does he realize its ability to explain many of the phenomena his keen eye has detected. Portmann often speaks of "mysteries"; one, for example, being what he considers the development of the antlers in many species of deer beyond the limits of necessity. But if a stag with outsized antlers secures more mates than his rivals, then his antlers are not an inch too long! Sure, they may inconvenience him at other times; but males are, within limits, expandable in a polygamous species, and the antlers are shed anyway.

"Animal Forms and Patterns" is a most stimulating and instructive book, even though sometimes its author merely puts us on the right track but is a little hesitant about following it to the logical destination.

[1] Animal Forms and Patterns by Adolf Portmann. Faber and Faber Ltd., London, 1952: 1–246, figs. 1–117. [Translation of "Die Tiergestalt," 1948.]

EDITOR'S NOTES

S. S. E. Meetings at Gainesville, Florida

At the business meeting of the Society for the Study of Evolution, September 8, 1954, affirmative action was taken upon a motion that the titles of papers read at the scientific sessions of the Society be published in Evolution. Some of the papers eventually find their way into the pages of Evolution, but the majority appears elsewhere, where they may be missed by many of the members. As a permanent record of the papers presented, the following list is reprinted from the Bulletins of the A. I. B. S. in order of presentation:

Young, Frank N., Indiana University, Bloomington, Ind. Variation in Relation to Isolation in the Genus *Polopinus* (Coleoptera: Tenebrionidae).

Stalker, H. D., Washington University, St. Louis, Mo. Cytology of the Parthenogenetic Fly, *Lonchoptera dubia*.

Michener, Charles D., and R. R. Sokal, University of Kansas, Lawrence, Kan. A Quantitative Approach to a Problem in Classification.

Blair, W. Frank, University of Texas, Austin, Texas. Natural Interbreeding between Speciating Populations of Microhylid Frogs.

Hinton, Taylor, University of California, Los Angeles, Calif. Multi-allelic Lethal Chromosomes in Wild Populations of *Drosophila melanogaster*.

Dyson-Hudson, V. R. (Demerec), Oxford University, England. The Ecology of Two British Species of the *obscura* group of *Drosophila*.

A. S. Romer, Harvard University, Cambridge, Mass. Fossil History.

R. A. Howard, Harvard University, Cambridge, Mass. Recent Flora.

T. H. Hubbell, University of Michigan, Ann Arbor, Mich. Recent Fauna.

Steiner, Erich, University of Michigan, Ann Arbor, Mich. The Evolution *Oenothera* in Middle America.

Löve, Askell, University of Manitoba, Winnipeg, Canada. Foundations of Cytotaxonomy.

Vickery, Robert K., Jr., University of Utah, Salt Lake City, Utah. The *Mimulus cardinalis Complex* (Scrophulariaceae).

Russell, Norman H., Grinnell College, Grinnell, Iowa. Variation Patterns in the Stemless White Violets.

Menzel, Margaret Y., and Meta S. Brown, Texas Agricultural Experiment Station, College Station, Texas. Compatibility Relationships of *Gossypium gossypioides*.

Pauley, Scott, S., Cabot Foundation, Harvard University, Petersham, Mass. Natural Hybridization of Trembling and Largetooth Aspen.

The editor also sought the sense of the meeting concerning inclusion of an occasional "Editor's Page" in Evolution, to provide for better communication between his office and the readers. The reaction was in general favorable and, thus, from time to time, such a page will be included in Evolution. At present, formal communication with the editor's office is limited in large part to contacts with contributors and the referees who graciously give their time to aid in so many ways with manuscripts. An issue seems to go forth into a vacuum from which there is no return. Only rumblings along the grapevine and the status of the membership list provide clues to the fate of our efforts. We would welcome comments and criticisms that would aid in our efforts to maintain and improve the standards of Evolution.

The journal is ultimately dependent upon the manuscripts that are submitted. The panel of Associate Editors does an excellent job of channeling papers to Evolution, but this group cannot possibly know of all the important work that is being done in the field. A constant vigilance by the readers for outstanding research in evolution and an effort to see that the results are submitted to Evolution can do more than any other single action to improve the journal. Since it was founded some eight years ago, Evolution has played a worthy role in communication, but there can be few who do not feel that its importance can be greatly increased. This first of the Editor's Notes is a plea for aid in this direction.

ZOOLOGY - BOTANY
LIBRARY
COLUMBIA UNIVERSITY

EVOLUTION

COLUMBIA UNIVERSITY
LIBRARIES
APR - 1954

INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

Vol. VIII *March 1954* No. 1

Cop. 1

CONTENTS

Geographic Speciation in Tropical Echinoids. ERNST MAYR 1

Trends in Geographic Variation in Palaearctic Members of the Genus *Parus*. D. W. SNOW 19

Physiological Properties of Gene Arrangement Carriers in *Drosophila persimilis* III. Cytoplasmic Influence on Fecundity of Arrangement Heterozygotes. ELIOT B. SPIESS 29

Evolution of Feeding Preferences in Phytophagus Insects. V. G. DETHIER 32

Statistics and the Evolution of Dicotyledons. K. R. SPORNE 55

Isolation in *Musa*, Sections Eumusa and Rhodochlamys. N. W. SIMMONDS 65

Population Dynamics and Evolution. BJÖRN KURTÉN 75

Notes and Comments

Revision of the Florissant Flora. DANIEL I. AXELROD 82

How Many Species? ANDRÉ CAILLEUX 83

Experimental Biology and Evolution. EVERETT C. OLSON 84

The Major Features of Evolution. EVERETT C. OLSON 87

PUBLISHED QUARTERLY

BY THE SOCIETY FOR THE STUDY OF EVOLUTION

PRINCE AND LEMON STREETS, LANCASTER, PA.

AND THE UNIVERSITY OF CHICAGO, CHICAGO 37, ILLINOIS

ISSUED MARCH 31, 1954

CURTIS NUMBER

EDITOR'S NOTES

S. S. E. Meetings at Gainesville, Florida

At the business meeting of the Society for the Study of Evolution, September 8, 1954, affirmative action was taken upon a motion that the titles of papers read at the scientific sessions of the Society be published in Evolution. Some of the papers eventually find their way into the pages of Evolution, but the majority appears elsewhere, where they may be missed by many of the members. As a permanent record of the papers presented, the following list is reprinted from the Bulletins of the A. I. B. S. in order of presentation:

Young, Frank N., Indiana University, Bloomington, Ind. Variation in Relation to Isolation in the Genus *Palaprus* (Coleoptera: Terebrionidae).

Stalker, H. D., Washington University, St. Louis, Mo. Cytology of the Lesser Migenetic Fly, *Limnophora fuliva*.

Michener, Charles D., and R. R. Sokal, University of Kansas, Lawrence, Kan. A Quantitative Approach to a Problem in Classification.

Blair, W. Frank, University of Texas, Austin, Texas. Natural Interbreeding between Sympatric Populations of Microtid Mice.

Hinton, Taylor, University of California, Los Angeles, Calif. Multifactorial Lethal Chromosomes in Wild Populations of *Drosophila melanogaster*.

Dyson-Hudson, V. R. (Demeree), Oxford University, England. The Ecology of Two British Species of the *obscura* group of *Drosophila*.

A. S. Romer, Harvard University, Cambridge, Mass. Fossil History.

R. A. Howard, Harvard University, Cambridge, Mass. Recent Flora.

T. H. Hubbell, University of Michigan, Ann Arbor, Mich. Recent Fauna.

Steiner, Erich, University of Michigan, Ann Arbor, Mich. The Evolution of Anolis in Middle America.

Love, Askell, University of Manitoba, Winnipeg, Canada. Formulations of Cytotaxonomy.

Vickery, Robert K., Jr., University of Utah, Salt Lake City, Utah. The *Gratiolus ardisoides* Complex (Scrophulariaceae).

Russell, Norman H., Grinnell College, Grinnell, Iowa. Variation Patterns in the Stemless White Violets.

Menzel, Margaret Y., and Meta S. Brown, Texas Agricultural Experiment Station, College Station, Texas. Compatibility Relationships of *Oenothera organensis*.

Pauley, Scott, S., Cabot Foundation, Harvard University, Petersham, Mass. Natural Hybridization of Trembling and Largetooth Aspen.

The editor also sought the sense of the meeting concerning inclusion of occasional "Editor's Page" in Evolution, to provide for better communication between the editor and the readers. The reaction was in general favorable and, thus, from time to time, such a page will be included in Evolution. At present, formal communication with the editor's office is limited to large part to exchanges with contributors and the referees who graciously give their time to aid in many ways with manuscripts. An editor seems to get into a vacuum from which there is no return. Only rumblings along the grapevine and the stams of the membership list provide clues to the fate of our efforts. We would welcome comments and criticisms that would aid in our efforts to maintain and improve the standards of Evolution.

The journal is ultimately dependent upon the manuscripts that are submitted. The panel of Associate Editors does an excellent job of reviewing papers in Evolution, but this group cannot possibly know of all the important work that is being done in the field. A constant vigilance by the readers for outstanding research in evolution and an effort to see that the results are submitted to Evolution can do more than any other single action to improve the journal. Since it was founded some eight years ago, Evolution has played a worthy role in communication, but there can be few who do not feel that its importance can be greatly increased. This first of the Editor's Notes is a plea for aid in this direction.

ZOOLOGY - BOTANY
LIBRARY
COLUMBIA UNIVERSITY

EVOLUTION

COLUMBIA UNIVERSITY
LIBRARIES
APR - 1954

INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

Vol. VIII *March 1954* No. 1

Cop. 1

CONTENTS

Geographic Speciation in Tropical Echinoids. ERNST MAYR 1

Trends in Geographic Variation in Palaearctic Members of the Genus *Parus*. D. W. SNOW 19

Physiological Properties of Gene Arrangement Carriers in *Drosophila persimilis* III. Cytoplasmic Influence on Fecundity of Arrangement Heterozygotes. ELIOT B. SPIESS 29

Evolution of Feeding Preferences in Phytophagus Insects. V. G. DETHIER 32

Statistics and the Evolution of Dicotyledons. K. R. SPORNE 55

Isolation in *Musa*, Sections Eumusa and Rhodochlamys. N. W. SIMMONDS 65

Population Dynamics and Evolution. BJÖRN KURTÉN 75

Notes and Comments

Revision of the Florissant Flora. DANIEL I. AXELROD 82

How Many Species? ANDRÉ CAILLEUX 83

Experimental Biology and Evolution. EVERETT C. OLSON 84

The Major Features of Evolution. EVERETT C. OLSON 87

PUBLISHED QUARTERLY

BY THE SOCIETY FOR THE STUDY OF EVOLUTION

PRINCE AND LEMON STREETS, LANCASTER, PA.

AND THE UNIVERSITY OF CHICAGO, CHICAGO 37, ILLINOIS

ISSUED MARCH 31, 1954

CURRENT NUMBER

EDITORIAL BOARD

EVERETT C. OLSON, *Editor*

ASSOCIATE EDITORS

Class of 1954

A. BRITO DA CUNHA, *São Paulo*
A. J. CAIN, *Oxford*
P. J. DARLINGTON, *Cambridge (Mass.)*
J. T. GREGORY, *New Haven*
H. LEWIS, *Los Angeles*
A. K. MILLER, *Iowa City*

Class of 1955

D. AMADON, *New York*
P. E. CLOUD, JR., *Washington, D. C.*
C. DE PAULA COUTO, *Rio de Janeiro*
J. F. CROW, *Madison*
E. B. FORD, *Oxford*
J. T. ROBINSON, *Pretoria*

Class of 1956

D. D. DAVIS, *Chicago*
S. LECLERCQ, *Liege*
H. LOWENSTAM, *Pasadena*
E. PERCIVAL, *Christchurch (N. Z.)*
N. TINBERGEN, *Oxford*
B. WALLACE, *Cold Spring Harbor*

EVOLUTION is published quarterly by the Society for the Study of Evolution at Prince and Lemon Sts., Lancaster, Pa., and American Museum of Natural History, New York 24, N. Y. Membership fee is $5.00 per year, of which $4.00 is for subscription to EVOLUTION. Subscription price to non-members: $6.00 per volume.

EVOLUTION is open to papers of evolutionary interest. Manuscripts and all editorial correspondence should be addressed to the Editor, Everett C. Olson, Walker Museum, University of Chicago, Chicago 37, Illinois. Subscriptions are to be ordered through the office of the Treasurer, Mr. C. M. Bogert, The American Museum of Natural History, New York 24, N. Y.

Numbers lost in the mail will be supplied free if written claim is received within one month of the date of issue of the next succeeding number.

Notices of change of address should be sent to the Treasurer. Directions for the mailing of reprints should be addressed to EVOLUTION, Prince and Lemon Streets, Lancaster, Pennsylvania.

Entered as second-class matter December 20, 1947, at the post-office at Lancaster, Pa., under the Act of March 3, 1879.

COLUMBIA UNIVERSITY
LIBRARIES
JUN 3 1954

EVOLUTION

INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

ZOOLOGY - BOTANY
LIBRARY
COLUMBIA UNIVERSITY

Vol. VIII *June 1954* No. 2

CONTENTS

Environmental Selection by *Drosophila* Mutants. C. H. Waddington 89

The Coral Snake Mimic Problem. Emmett Reid Dunn 97

Reticulate Evolution in Appalachian Aspleniums. Warren H. Wagner jr. 103

A Further Study of Chromosomal Polymorphism in *Drosophila willistoni* in Its Relation to Environment. A. Brito da Cunha and Theodosius Dobzhansky 119

Comparable Mutant Eye Colors in *Mormoniella* and *Pachycrepoideus* (Hymenoptera: Pteromalidae). P. W. Whiting 135

Interfertile Sibling Species in the *willistoni* Group of *Drosophila*. Hampton L. Carson 148

Evidence of Tooth Structure on the Relationships of the Early Groups of Carnivora. Loris S. Russell 166

Experimental Studies of the Distribution of Gene Frequencies in Very Small Populations of *Drosophila melanogaster*, I. Forked. Warwik E. Kerr and Sewall Wright 172

Notes and Comments

Fundamentals of Ecology. Richard S. Miller 178

Gene Dispersal and Ethology of the Rhinocerotidae. G. E. Hutchinson and S. Dillon Ripley 178

PUBLISHED QUARTERLY

BY THE SOCIETY FOR THE STUDY OF EVOLUTION

PRINCE AND LEMON STREETS, LANCASTER, PA.

AND THE UNIVERSITY OF CHICAGO, CHICAGO 37, ILLINOIS

ISSUED JUNE 17, 1954

CURRENT NUMBER

EDITORIAL BOARD

EVERETT C. OLSON, *Editor*

ASSOCIATE EDITORS

Class of 1954

A. BRITO DA CUNHA, *São Paulo*
A. J. CAIN, *Oxford*
P. J. DARLINGTON, *Cambridge (Mass.)*
J. T. GREGORY, *New Haven*
H. LEWIS, *Los Angeles*
A. K. MILLER, *Iowa City*

Class of 1955

D. AMADON, *New York*
P. E. CLOUD, JR., *Washington, D. C.*
C. DE PAULA COUTO, *Rio de Janeiro*
J. F. CROW, *Madison*
E. B. FORD, *Oxford*
J. T. ROBINSON, *Pretoria*

Class of 1956

D. D. DAVIS, *Chicago*
S. LECLERCQ, *Liege*
H. LOWENSTAM, *Pasadena*
E. PERCIVAL, *Christchurch (N. Z.)*
N. TINBERGEN, *Oxford*
B. WALLACE, *Cold Spring Harbor*

EVOLUTION is published quarterly by the Society for the Study of Evolution at Prince and Lemon Sts., Lancaster, Pa., and American Museum of Natural History, New York 24, N. Y. Membership fee is $5.00 per year, of which $4.00 is for subscription to EVOLUTION. Subscription price to non-members: $6.00 per volume.

EVOLUTION is open to papers of evolutionary interest. Manuscripts and all editorial correspondence should be addressed to the Editor, Everett C. Olson, Walker Museum, University of Chicago, Chicago 37, Illinois. Subscriptions are to be ordered through the office of the Treasurer, Mr. C. M. Bogert, The American Museum of Natural History, New York 24, N. Y.

Numbers lost in the mail will be supplied free if written claim is received within one month of the date of issue of the next succeeding number.

Notices of change of address should be sent to the Treasurer. Directions for the mailing of reprints should be addressed to EVOLUTION, Prince and Lemon Streets, Lancaster, Pennsylvania.

Entered as second-class matter December 20, 1947, at the post-office at Lancaster, Pa., under the Act of March 3, 1879.

ZOOLOGY - BOTANY
LIBRARY
COLUMBIA UNIVERSITY
COLUMBIA UNIVERSITY COPY 1
LIBRARIES
SEP 1954

EVOLUTION

INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

Vol. VIII *September 1954* No. 3

CONTENTS

Phylogenetic Aspects of Respiratory Function. F. H. McCutcheon 181

Further Serological Data on the Relationships of Some Decapod Crustacea. Charles A. Leone 192

A Partial Breakdown of Temporal and Ecological Isolation between Choristoneura Species (Lepidoptera, Torticidae). Stanley G. Smith 206

Experimental Studies on the Distribution of Gene Frequencies in Very Small Populations of *Drosophila melanogaster*. Sewall Wright and Warwick E. Kerr 225

Integration of the Genotype in Local Populations of Three Species of *Drosophila*. M. Vetukhiv 241

Hybridization in the Red-Eyed Towhees of Mexico. Charles G. Sibley 252

Notes and Comments

Population Size and Effectiveness of Selection. Everett R. Dempster and Michael Lerner 291

Comment on Note by Dempster and Lerner on Population Size and Effectiveness of Selection. Björn Kurtén 292

CURRENT NUMBER

PUBLISHED QUARTERLY

BY THE SOCIETY FOR THE STUDY OF EVOLUTION

PRINCE AND LEMON STREETS, LANCASTER, PA.

AND THE UNIVERSITY OF CHICAGO, CHICAGO 37, ILLINOIS

ISSUED SEPTEMBER 24, 1954

EDITORIAL BOARD

EVERETT C. OLSON, *Editor*

ASSOCIATE EDITORS

Class of 1954

A. BRITO DA CUNHA, *São Paulo*
A. J. CAIN, *Oxford*
P. J. DARLINGTON, *Cambridge (Mass.)*
J. T. GREGORY, *New Haven*
H. LEWIS, *Los Angeles*
A. K. MILLER, *Iowa City*

Class of 1955

D. AMADON, *New York*
P. E. CLOUD, JR., *Washington, D. C.*
C. DE PAULA COUTO, *Rio de Janeiro*
J. F. CROW, *Madison*
E. B. FORD, *Oxford*
J. T. ROBINSON, *Pretoria*

Class of 1956

D. D. DAVIS, *Chicago*
S. LECLERCQ, *Liege*
H. LOWENSTAM, *Pasadena*
E. PERCIVAL, *Christchurch (N. Z.)*
N. TINBERGEN, *Oxford*
B. WALLACE, *Cold Spring Harbor*

EVOLUTION is published quarterly by the Society for the Study of Evolution at Prince and Lemon Sts., Lancaster, Pa., and American Museum of Natural History, New York 24, N. Y. Membership fee is $5.00 per year, of which $4.00 is for subscription to EVOLUTION. Subscription price to non-members: $6.00 per volume.

EVOLUTION is open to papers of evolutionary interest. Manuscripts and all editorial correspondence should be addressed to the Editor, Everett C. Olson, Walker Museum, University of Chicago, Chicago 37, Illinois. Subscriptions are to be ordered through the office of the Treasurer, Mr. C. M. Bogert, The American Museum of Natural History, New York 24, N. Y.

Numbers lost in the mail will be supplied free if written claim is received within one month of the date of issue of the next succeeding number.

Notices of change of address should be sent to the Treasurer. Directions for the mailing of reprints should be addressed to EVOLUTION, Prince and Lemon Streets, Lancaster, Pennsylvania.

Entered as second-class matter December 20, 1947, at the post-office at Lancaster, Pa., under the Act of March 3, 1879.

ZOOLOGY - BOTANY
LIBRARY
COLUMBIA UNIVERSITY
COPY 1
JAN 4 - 1955

EVOLUTION

INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

Vol. VIII *December 1954* No. 4

CONTENTS

Experimental Studies of the Distribution of Gene Frequencies in Very Small Populations of *Drosophila melanogaster* III. Aristapedia and Spineless. WARWICK E. KERR and SEWALL WRIGHT .. 293

The Genetic Population Structure of Brazilian *Drosophila willistoni*. C. PAVAN and E. N. KNAPP 303

Natural Hybridization in the *Peromyscus leucopus* Species Group of Mice. W. H. MCCARLEY 314

Prehominid Dentition and Hominid Evolution. J. T. ROBINSON .. 324

Interaction of Adaptive Values in Polymorphic Experimental Populations of *Drosophila pseudoobscura*. HOWARD LEVENE, OLGA PAVLOVSKY, and THEODOSIUS DOBZHANSKY 335

An Extreme Form of Chiasma Localization in a Species of *Bryodema* (Orthoptera, Acrididae). M. J. D. WHITE 350

Evolution and Chromosomes in Intergeneric Pheasant Hybrids. GUNNAR C. SANDNES 359

Categories of Adaptation. GARTH UNDERWOOD 365

Hybridization as an Evolutionary Mechanism. E. ANDERSON and G. L. STEBBINS 378

The Foramen Ovale. TILLY EDINGER and DAVID B. KITTS 389

Notes and Comments

Animal Forms and Patterns. DEAN AMADON 405

Editor's Notes

S. S. E. Meetings at Gainesville, Florida 406

Index, Volume VIII v

PUBLISHED QUARTERLY

BY THE SOCIETY FOR THE STUDY OF EVOLUTION

PRINCE AND LEMON STREETS, LANCASTER, PA.

AND THE UNIVERSITY OF CHICAGO, CHICAGO 37, ILLINOIS

ISSUED DECEMBER 30, 1954

EDITORIAL BOARD

EVERETT C. OLSON, *Editor*

ASSOCIATE EDITORS

Class of 1954

A. BRITO DA CUNHA, *São Paulo*
A. J. CAIN, *Oxford*
P. J. DARLINGTON, *Cambridge (Mass.)*
J. T. GREGORY, *New Haven*
H. LEWIS, *Los Angeles*
A. K. MILLER, *Iowa City*

Class of 1955

D. AMADON, *New York*
P. E. CLOUD, JR., *Washington, D. C.*
C. DE PAULA COUTO, *Rio de Janeiro*
J. F. CROW, *Madison*
E. B. FORD, *Oxford*
J. T. ROBINSON, *Pretoria*

Class of 1956

D. D. DAVIS, *Chicago*
S. LECLERCQ, *Liege*
H. LOWENSTAM, *Pasadena*
E. PERCIVAL, *Christchurch (N. Z.)*
N. TINBERGEN, *Oxford*
B. WALLACE, *Cold Spring Harbor*

EVOLUTION is published quarterly by the Society for the Study of Evolution at Prince and Lemon Sts., Lancaster, Pa., and American Museum of Natural History, New York 24, N. Y. Membership fee is $5.00 per year, of which $4.00 is for subscription to EVOLUTION. Subscription price to non-members: $6.00 per volume.

EVOLUTION is open to papers of evolutionary interest. Manuscripts and all editorial correspondence should be addressed to the Editor, Everett C. Olson, Walker Museum, University of Chicago, Chicago 37, Illinois. Subscriptions are to be ordered through the office of the Treasurer, Mr. C. M. Bogert, The American Museum of Natural History, New York 24, N. Y.

Numbers lost in the mail will be supplied free if written claim is received within one month of the date of issue of the next succeeding number.

Notices of change of address should be sent to the Treasurer. Directions for the mailing of reprints should be addressed to EVOLUTION, Prince and Lemon Streets, Lancaster, Pennsylvania.

Entered as second-class matter December 20, 1947, at the post-office at Lancaster, Pa., under the Act of March 3, 1879.

Contributions to EVOLUTION may be in the fields of genetics, cytology, plant and animal taxonomy, paleontology, ecology, anthropology, bacteriology, or any other field of biology, provided that the facts and conclusions presented are of primary interest to the student of evolution. Descriptive material shall be included only so far as it is the basis of the evolutionary conclusions. Manuscripts are examined for suitability by members of the Editorial Board or other competent critics.

The length of manuscripts will be limited to twenty printed pages, unless an exception is granted by the Editorial Board. Short manuscripts and discussions will be included in a separate section, "Notes and Comments." Half tones and tabular material will have to be kept within economic limits.

Proof should be corrected immediately on receipt, and returned at once with manuscript *to the Editor.* Authors should leave forwarding directions whenever they move away from the address sent with the manuscript. Ordinarily page proof will not be sent to the author. Costs of changes in proof from the original copy will be charged to the author.

Reprints should be ordered when galley proof is returned. Illustrations and cuts will be destroyed, unless their return is requested on the reprint order.

PREPARATION OF MANUSCRIPT

Manuscripts should be typewritten in double spacing with ample margins and on only one side of the paper. The Editor should have one carbon copy in addition to the original manuscript. The author should keep one carbon copy.

Legends of figures, *as well as all tables,* should be typed on separate sheets. The captions for several figures may be placed on a single sheet.
Illustrations, including maps, should be referred to as "figures" wherever possible. Plates are reserved for illustrations that require paper inserts or for collections of small figures. All figures and plates are reduced to a maximum of 4⅞ inches in width and 6½ inches in length. Reductions may be stated in the caption but not on the figure.

All references to literature should be collected into a list of "Literature Cited" at the end of the article. See recent numbers of EVOLUTION for accepted style.

Titles should be short, preferably less than seven words. Footnote material should be incorporated in the text whenever possible.

Every article of more than a few pages should have a summary limited to four per cent of the length of the paper; it is to be complete in itself, and understandable without reference to the body of the article. The scope of the paper should be stated in an introductory paragraph.

Authors are requested to prepare abstracts of their papers to be returned with the proof to the Editor to be forwarded to Biological Abstracts.

Manuscripts should be addressed to

Dr. Everett C. Olson
Walker Museum, Univ. of Chicago
Chicago 37, Ill.

THE SOCIETY FOR THE STUDY OF EVOLUTION

Officers for 1954

President: KARL P. SCHMIDT, Chicago Natural History Museum, Chicago 5, Illinois

Vice Presidents: CARLOS G. AGUAYO, 4 No. 554 Vedado, Havana, Cuba
LEE R. DICE, University of Michigan, Ann Arbor, Michigan
THEODORE JUST, Chicago Natural History Museum, Chicago 5, Illinois

Secretary (1953–1955): HARLAN LEWIS, University of California, Los Angeles 24, California

Treasurer (1955–1957): W. FRANK BLAIR, University of Texas, Austin 12, Texas

Editor (1953–1955): EVERETT C. OLSON, The University of Chicago, Chicago 37, Illinois

Elected Members of the Council:

Class of 1954: A. H. MILLER (Berkeley), S. WRIGHT (Chicago)
Class of 1955: I. W. BAILEY (Cambridge), T. M. SONNEBORN (Bloomington)
Class of 1956: E. ANDERSON (St. Louis), G. G. SIMPSON (New York)

OBJECTS: The object of the Society for the Study of Evolution, which was founded in March, 1946, is the promotion of the study of organic evolution and the integration of the various fields of science concerned with evolution. The Society endeavors to accomplish this through the publication of the journal and through meetings and working committees.

MEMBERSHIP: Membership is open to all those who are interested in the study of evolution. Members are elected by the Council. There are three classes of members:

Members—Dues $5.00 (including subscription to EVOLUTION)
Sustaining Members—Dues $10.00
Patrons—Single fee $1,000.

All members in good standing receive EVOLUTION.

Election of officers and presentation of scientific papers will take place at the annual meeting. Special meetings may be called by the President with the approval of the Council.

Applications for membership should be directed to the Secretary, to whom all correspondence regarding membership should be addressed. Institutions may not become members but may subscribe to EVOLUTION. All checks should be made payable to The Society for the Study of Evolution.

1954
Inc